FEEDING ECOLOGY AND ENERGY DENSITY OF JUVENILE CHUM SALMON, ONCORHYNCHUS KETA, FROM KUSKOKWIM BAY, WESTERN ALASKA

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A

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GENERAL ABSTRACT

Juvenile chum salmon from Kuskokwim Bay were sampled for patterns in diet and energy density in 2003 and 2004. Comparisons were made interannually, seasonally, between juvenile size classes, and between sailinity ranges. Sampling was conducted using a modified Kvichak Trawl. Bomb calorimetry was used to obtain energy density values.

Feeding success and feeding intensity increased with fish size and season, and was highest in waters with moderate salinity. Feeding success and intensity were lowest for smaller juvenile chum salmon collected early in the season in water with low salinity. Prey composition was similar in both years, but varied with fish size, salinity ranges, and sampling weeks. Calanoid copepods and insects combined made up >50% of all prey items consumed and >80% of the overall prey biomass for all size classes, salinity ranges, and weeks. Feeding by juvenile chum salmon in Kuskokwim Bay appeared to be opportunistic.

In 2003, no significant differences in energy density were found. In 2004, energy density decreased significantly from mid-May to mid-June and with increasing fish size. Decreasing energy density with season and size suggests that juvenile chum salmon were allocating the majority of their energy towards growth and smoltification, rather than lipid storage.

Results from this study indicate that Kuskokwim bay may provide a suboptimal estuarine rearing habitat for juvenile chum salmon. If seasonally increasing energy demands are not balanced by an increasing food supply, the severe implications potentially include declines in growth rates and possibly overall survival probability of chum salmon juveniles in Kuskokwim Bay.

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GENERAL INTRODUCTION

Pacific salmon are a valuable ecological component and economic resource of the Pacific Oceans and adjacent watersheds. Seven species of salmon occur in the Pacific Ocean, including Chinook salmon (*Oncorhynchus tshawytscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), pink salmon (*O. gorbuscha*), masu salmon (*O. masou*), and amago salmon (*O. rhodurus*). The former five species reproduce in both Asia and North America, while the later two species only reproduce in Asia. All species of Pacific salmon spawn in fresh water, with the exception of some pink salmon that spawn in brackish waters. After hatching, most species of Pacific salmon migrate to the ocean after spending between 0-2 years in freshwater. Only some species remain in fresh water for their entire life (Quinn 2005). In many areas, Pacific salmon provide the main source of food and income for subsistence users, commercial and recreational fishermen.

Of all Pacific salmon species, chum salmon have the largest geographic distribution, ranging in North America from Monterey Bay in California to the Arctic coast east to the McKenzie River that empties into the Beaufort Sea, and in Asia from Korea to the Arctic coast of the Soviet Union and west to the Lena River which empties into the Laptev Sea (reviewed by Salo 1991). Chum salmon rank third in abundance after pink and sockeye salmon and generally reach maturity from 3 to 5 years of age. Chum salmon are second only to Chinook salmon in size. In almost all regions of chum salmon distributional range, summer and fall runs are common. As a general trend, summer chum salmon tend to spawn in the main stem of streams and tributaries, while fall chum tend to select areas of upwelling for spawning habitat (reviewed by Salo 1991).

Compared to other salmonids, chum salmon have a unique early life history. The seasonal migration of chum salmon fry to estuaries is a function of latitudinal distribution, with fish reaching estuaries earlier in the South. For example, chum fry in the Yukon River and Noatak River begin migration after ice-break up and peak during June and July (Martin et al 1986). In comparison chum fry migrate from Minter Creek,

Southern Puget Sound, from late January though late April (Salo & Noble 1954). Time spent in freshwater is much shorter for chum juveniles than for other salmon species, with the exception of pink salmon. Depending on distance required to reach estuaries, chum salmon fry can remain in fresh water for periods varying from a few days to several weeks. Residence time in estuarine waters is variable, depending on food availability, temperature, and size of juvenile fish (Healey 1979, Pearcy et al. 1989). Common prey items for juvenile chum salmon in nearshore waters include harpacticoid and calanoid copepods, larvaceans, and insects (Feller & Kaczynski 1975, Sibert 1979, Healy 1991, Sturdevant et al. 1996). Juvenile chum salmon are believed to be highly dependant on estuaries for both growth and physiological changes before entering the ocean environment (Simenstad & Salo 1980, Healy 1982b, Iwata & Komatsu 1984, Simenstad & Wissmar 1984).

Chum salmon are thought to experience the highest mortality rates during their early marine residence (Bakshtanskiy 1964, Healey 1982a, Whitmus 1985, Willette et al. 2001, Willette 2001, Fukuwaka & Suzuki 2002). Dispersal, feeding success, growth, and predation are all processes believed to be critical elements affecting survival during the early marine life (Walters et al. 1978). In Pacific salmon, juveniles undergo energetically costly physiological changes as they adjust to marine water during the estuarine outmigration (Iwata & Komatsu 1984). In the Nanaimo estuary, British Columbia, poor feeding conditions were hypothesized as a possible reason for the early emigration of juvenile chum salmon (Healey 1979). Cohorts of smaller juvenile chum salmon tend to reside longer in estuaries (Pearcy et al. 1989). Because smaller juveniles depend more on estuaries than larger juveniles, an early emigration time may have a negative impact on their survival success (Roughgarden et al. 1988). Densities of predators, many of which are size selective (Bakshtanskiy 1964, Willette 2001, Fukuwaka & Suzuki 2002), make it necessary for juvenile salmonids to allocate the majority of their consumed energy towards growth in order to reduce the period during which the fish are susceptible to high rates of size-selective mortality. Reduced growth rates will extend the period of highest

susceptibility to size-selective predation, and may ultimately determine year-class strength (Healey 1982a, Willette 2001).

The Kuskokwim River and its tributaries provide spawning habitat for summer and fall chum salmon populations (Seeb et al. 1997, Gilk et al. 2005). Weir studies and information from area residents describe the spawning migration as lasting from June through October (Gilk et al. 2005). Residents of western Alaska rely on salmon returns for a major part of their subsistence needs and chum salmon make up a sizeable portion of their overall harvest. Poor chum salmon returns to the Kuskokwim River watershed have caused much concern in past years (ADF&G 2000). In 1997, 1998, 2000, and 2001 this region was declared an economic disaster by the Governor of the State of Alaska due to the low numbers of chum salmon returning to the system. In 2000, the Kuskokwim River chum salmon populations were declared a stock of concern (ADF&G 2000, Burkey et al. 2000). Since then, chum salmon returns have strengthened to much higher levels (Linderman & Bergstrom 2006); however neither the reasons for the declines nor the rebounding of the chum salmon populations are known. In addition, so little is known about the ecology of chum salmon in western Alaska, that it is difficult to develop or test hypotheses regarding mechanisms responsible for population regulation.

Information on the early life history of juvenile chum salmon from the Kuskokwim watershed is lacking. Few studies have focused on emergence timing and freshwater ecology, but information on the estuarine ecology of juvenile chum salmon in Kuskokwim Bay is missing. This study will focus on patterns in the diet and energy density of juvenile chum salmon while residing in Kuskokwim Bay to fill this gap in knowledge concerning early life history. Research results from this study will be valuable information that may be used for future management of this essential natural resource.

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Feeding ecology of juvenile chum salmon (*Oncorhynchus keta*) in Kuskokwim Bay, Western Alaska[1]

Sean E. Burril*, Nicola Hillgruber, and Chris Zimmerman

ABSTRACT: Juvenile chum salmon from Kuskokwim Bay in western Alaska were sampled in two years, in 2003 (n = 54) and in 2004 (n = 358), to examine juvenile feeding success and patterns of prey composition and selection. Sampling was conducted using a modified Kvichak Trawl. Feeding success was variable and differed with size, season, salinity, and year. Feeding success increased with size and season. Numerically and gravimetrically measured feeding intensity increased with size and week, and was highest in waters with moderate salinity ranging from 5-19. Feeding success and intensity were lowest for the smallest size class of juvenile chum salmon that were collected early in the season and in water with low salinity ranging from 0-4. Prey composition was similar in both years, but varied with chum salmon size, salinity ranges, and sampling weeks. Small calanoid copepods (<2.5mm), harpacticoid copepods, and drift insects were the primary prey items for juvenile chum salmon. Calanoid copepods and insects combined made up > 50% of all prey items consumed and > 80% of the overall prey biomass for all size classes, salinity ranges, and weeks. No statistically significant pattern in diel feeding rhythm was detected. With the exception of a positive selection for small calanoid copepods, feeding by juvenile chum salmon in Kuskokwim Bay appeared to be opportunistic. Results from this study indicate that Kuskokwim bay may provide a suboptimal estuarine rearing habitat for juvenile chum salmon.

KEY WORDS: Feeding ecology, chum salmon, estuary, Kuskokwim Bay

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INTRODUCTION

Early marine mortality is a major factor impacting the population abundance of salmonids (Bakshtanskiy 1964, Healey 1982a, Whitmus 1985, Willette 2001, Willette et al. 2001, Fukuwaka & Suzuki 2002). Dispersal, feeding success, growth, and predation are all believed to be critical elements that affect survival during the early marine life (Walters et al. 1978). Recruitment success is thought to be associated with growth rates during the period of estuarine residence. Consequently, analysis of juvenile feeding habits may provide the first information about the survival probability of members of salmonid populations. The smaller members of a cohort of juvenile salmon in particular, suffer the highest mortality rates (Ricker 1962, Parker 1971, Simenstad & Salo 1980, Healy 1982a, Simenstad & Wissmar 1984, reviewed by Pearcy et al. 1989). In the Nanaimo estuary, British Columbia, for example, poor feeding conditions were hypothesized as a possible reason for the early emigration of juvenile chum salmon (*Oncorhynchus keta*; Healey 1979). Cohorts of smaller juvenile Chinook (*O. tshawytscha*; Fisher & Pearcy 1995) and chum salmon (Pearcy et al. 1989) had longer residence time in estuaries. Because smaller juveniles depend more on estuaries than larger juveniles, an early emigration time may diminish survival success (Roughgarden et al. 1988).

Pacific salmon are thought to be mainly opportunistic foragers (Healey 1982b). In spite of this, diet composition seldom reflects the most abundant prey items in the environment (Schabetsberger et al. 2003), suggesting a trade-off between selection for the most abundant and the most energetically valuable prey items. Both the quantity (Brett 1995) and the caloric value (Cho 1983, Higgs et al. 1995) of prey consumed can affect juvenile condition and growth rates. Reduced growth rates will extend the period of highest susceptibility to size-selective predation, and may ultimately determine year-class strength (Healey 1982a, Willette 2001).

Juvenile chum salmon enter estuaries at a smaller size than most other Pacific salmon, with the exception of pink salmon (*O. gorbuscha*). Estuarine residence may be more critical to the survival of juvenile chum salmon than any other salmon species, with

the exception of Chinook salmon (Healey 1982b). Common prey items for juvenile chum salmon in estuarine waters are harpacticoid and calanoid copepods, gammarid amphipods, insects, and cladocerans (Feller & Kaczynski 1975, Sibert 1979, Salo 1991, Higgs et al. 1995, Sturdevant et al. 1996, Moulton 1997). Epibenthic prey species are common in the diets of smaller chum salmon, while larger juveniles tend to switch to planktonic prey (Feller & Kaczynski 1975, Wissmar & Simenstad 1988).

Chum salmon returns to the Kuskokwim River had low numbers over the last decade (ADF&G 2000). To date, no data are available on the early marine ecology of juvenile chum salmon in Kuskokwim Bay. Changes in estuarine feeding may have contributed to poor marine survival and may ultimately have resulted in poor year-class strength, but, due to the gap in knowledge about this important period, any hypotheses on population regulation of western Alaska chum salmon are difficult to evaluate.

Specifically, the goal for this study was to examine the feeding ecology of juvenile chum salmon in Kuskokwim Bay, Alaska. The objectives for this study were (1) to examine the feeding habits of juvenile chum salmon from Kuskokwim Bay by size, season, salinity and year, (2) to describe differences in prey composition and selection between years (2003 and 2004), weeks (2004), size classes (2003 and 2004), and habitat salinity ranges (2004), and (3) to examine diel feeding patterns (2004) in juvenile chum salmon during their residence in Kuskokwim Bay.

METHODS AND MATERIALS

Study area

Kuskokwim Bay (Figure 1) is a large, shallow estuary bordering the southeastern Bering Sea, between Bristol Bay to the Southeast and Norton Sound to the Northwest (latitude: 60° 15' to 58° 30'; longitude: 162° 00' to 162° 30'). The depth throughout much of the bay is between 2 and 6 m. The estuary receives freshwater from the Kuskokwim River, the second largest drainage in Alaska. Estuarine sea surface temperature and salinity indicate a southerly outflow of the Kuskokwim River into the

bay with the river plume extending along the eastern estuary shore. Due to the input of the Kuskokwim River, a glacially fed river with a high silt load, much of the bay is very turbid.

Kuskokwim Bay provides a migratory pathway and possibly nursery environment to all five species of Pacific salmon, including pink, chum, sockeye (*O. nerka*), coho (*O. kisutch*) and Chinook salmon.

Field methods

Samples were collected aboard the S/V 'Eileen O'Farrel' in 2003 and the F/V 'Namorada' in 2004. All samples were collected within Kuskokwim Bay, on a station grid of 22 stations. Stations were regularly spaced every 15 minutes of latitude and every 7.5 minutes of longitude in an attempt to get thorough sampling coverage of the bay. Fish sampling was conducted with a modified Kvichak surface trawl (3.1m height x 6.1m width x 15.0m length) during daylight hours. The Kvichak trawl, traditionally fished between two boats, was equipped with two doors to provide horizontal spread for the net. Floats at the headrope and weights at the footrope provided vertical spread and assured that the net fished at the surface.

In 2003, sampling was conducted monthly during three research cruises, June 23-25, July 24-26 and August 26-30 (Appendix A). In 2004, sampling began May 17 and continued until June 11. Zooplankton were collected with a 1 m^2 NIO Tucker Trawl equipped with 250 μm mesh (2003) or a 0.75 m diameter ring net equipped with 335 μm mesh (2004), both were fished for 5 minutes at the surface. Both plankton nets were equipped with a flowmeter so that the volume of water filtered could be calculated. Hydrographic data were collected with a SeaBird Electronics SBE-19 Seacat Conductivity-Salinity-Depth (CTD) profiler equipped with a Wetstar fluorometer and a D&A Instruments transmissometer (2004). In 2004, one 24-hour study was conducted at a single station with fish tows made every five hours for analysis of diel feeding patterns.

After recovery of the trawl, all fish collected were anesthetized in MS-222 prior to handling. All fish were identified to species and counted if the total catch was less than

500 fish. If the total catch exceeded 500 fish, all salmonids were removed and the remainder of the mixed species was weighed. A sub-sample of approximately 100 non-salmonid mixed species was identified, counted, measured and weighed and the total number and catch composition estimated. All chum salmon juveniles were measured for both standard (SL) and fork length (FL) to the nearest 1 mm and frozen.

Upon retrieval of the zooplankton net, the net bag was washed down to concentrate organisms in the cod-end, the cod-end detached and the zooplankton sample preserved in a 10% buffered formalin-seawater solution for later analysis.

Laboratory methods

Juvenile chum salmon were sorted into four 10-mm size classes: 30-39, 40-49, 50-59, and ≥ 60 mm FL. Ten individuals from each size class were selected for diet analysis. Wet weight of each fish was measured to the nearest 0.001 g using a Sartorius 300,00g/30,000g scale. Gill raker counts from the first gill arch were used to confirm species identification. Stomachs were dissected and prey items were removed from the cardiac and pyloric section of the stomach for analysis of juvenile diet. The weight of prey contents (mg wet weight), blotted to remove excess water, was then recorded as the difference between full and empty stomach weights. Fish were considered to have been feeding if their stomachs contained more than a trace of food. Stomach fullness codes were recorded as (1) empty stomach, (2) trace contents, and (3-6) 25%, 50%, 75%, or 100% full. All prey items were carefully removed, fixed in 10% formalin tap water solution for a minimum of 6 weeks, then preserved in 70% EtOH until diet analysis.

For the diet analysis, prey in the stomach contents were identified to the lowest taxonomic level practicable and counted. After teasing apart any prey clumps, a Folsom plankton splitter was used when necessary to reduce diet samples to a manageable size (100-200 individuals). Calanoid copepods were separated into large (≥2.5 mm total length TL) and small (<2.5 mm TL) size classes. Average wet weights for taxonomic groups were determined by taking wet weight averages of ≥100 individuals, retrieved

from literature (Boldt & Haldorson 2003), or provided by C. Stark (University of Alaska Fairbanks, personal communication).

All zooplankton samples were strained on a 45 μm sieve and rinsed several times with tap water to remove any trace of formalin. The whole sample was scanned for large, rare items. Plankton samples were then split into a manageable fraction volume with a Folsom plankton splitter. Splitting of the sample continued until a total count of 200-500 organisms was achieved. Detailed species composition of the sample was determined after splitting the sample. All zooplankton of one split sub-sample were identified to the lowest taxonomic level and developmental stage possible and counted. Copepods were sub-divided into two groups: <2.5 mm TL and ≥2.5 mm TL. For each new taxonomic group, a number of organisms was collected in vials and stored in 70% ethanol solution as voucher specimens for future reference.

Statistical methods

Data summaries and statistical analyses were conducted on sample collections by year, week, one 24-hour time period, salinity, and chum salmon size class. Diet analyses included measures of the quantity of prey consumed and measures of prey composition. Prey quantity was analyzed using mean total number and mean total weight of prey items from all non-empty stomachs, percent body weight (%BW = wet stomach content weight / (fish body weight - stomach content weight)) from all non-empty stomachs, stomach fullness index (Sturdevant et al. 2000), and feeding incidence (calculated as the numeric ratio of empty stomachs to total stomachs). Prey composition was described by percent number (%N) and percent weight (%W) of the total prey weight and percent frequency of occurrence (%FO) of prey categories, from all non-empty stomachs. Each of these three indices portrays a different aspect of the diet of chum salmon juveniles (Hyslop 1980). Percent N and %W were calculated as total number or weight of a given taxon divided by total number or weight of all taxa combined. Percent FO is a non-additive index that is calculated as the proportion of stomachs containing a given prey item (Cortés 1997). Diel

feeding habits were analyzed using %BW to account for prey ration (Brodeur & Pearcy 1987).

Prior to statistical testing, all diet data were examined for departures from the assumptions of analysis of variance (ANOVA). Non-normally distributed data were transformed with log (y + 1) for counts and arc-sin square root for percents and proportions to achieve homoscedasticity. ANOVA was used to test for differences in prey quantity and prey composition by year, week, size class, and salinity. Since both salinity and week were covariates with size class, a regression of FL, mean total prey number and mean total prey weight was performed and the residual values were used for analysis of variance. ANOVA was also used for the diel feeding study to test for differences in %BW over time. If significant differences were found at an alpha (α) of 0.05, a Scheffe's multiple comparison procedure was used to examine pairwise relationships.

Feeding selectivity was estimated using Chesson's α (Chesson 1978):

$$\hat{\alpha}_i = \frac{\frac{r_i}{n_i}}{\sum_{j=1}^{m} \frac{r_i}{n_i}}$$

where r_i is the number of food items of type i in the consumers diet, n_i is the total number of food of type i in the environment, and m is total number of prey taxa. Chesson's α was calculated for each individual chum salmon juvenile and averaged for a given length class (Fortier & Harris 1989). Chesson's α is superior to other selectivity indices such as Ivlev's, since it provides results that are independent of prey densities in the environment (Chesson 1978, 1983). Assuming Type 1 feeding selection, the results can be statistically tested for significance (Manly 1974):

$$g = \frac{\left(\hat{\beta}_i - \beta_i\right)^2}{\mathrm{var}\left(\hat{\beta}_i\right)^{1/2}}$$

where $\hat{\beta}_i$ is the average alpha, and β_i equals alpha value at which there is no selection (1/k; where k equals the number of prey categories). Since g follows a standard normal distribution, significance can be tested using a z-table.

RESULTS

General feeding patterns

Samples were limited in 2003 (n = 54) compared to 2004 (n = 358). The time frame and frequency of sampling also differed between years, samples were taken on June 23-25 and July 24-26 in 2003, and weekly from May 17 through June 11 in 2004. In 2003, only the 40-49 mm and 50-59 mm size classes were present.

Diets of 412 chum juveniles were examined in 2003 and 2004, 31 of 54 were feeding in 2003 (57% feeding incidence) and 290 of 358 in 2004 (81% feeding incidence). Chum salmon juveniles ranged in size from 42.0 mm to 59.0 mm FL in 2003 and from 31.0 mm to 66.0 mm FL in 2004. Mean size of juvenile chum salmon was significantly greater (t-test, $P < 0.05$) in 2003 (49.5 mm FL) than in 2004 (43.5 mm FL). During both years, size of juvenile chum salmon increased. In 2003, juvenile chum salmon from cruise 2 (July 24-26) were significantly longer ($P < 0.01$) than cruise 1 (June 23-25; Figure 1.2). In 2004, average chum salmon FL increased overall from 36.6 mm to 46.0 mm for weeks 1-4 (May 17-June 11), with significant differences ($P < 0.05$) between all weeks (Figure 1.3).

Twenty-five prey types were identified in the stomachs of chum salmon juveniles (Appendix A.). These were pooled into the most prominent prey categories in terms of abundance and biomass, namely calanoid and harpacticoid copepods, calanoid copepodites, and insects. All other prey taxa, except cyclopoids copepods, were combined into one category called "other". For the scope of this study, only six prey categories were used to describe the diet and ten categories to describe feeding selectivity (Tables 1.3 and 1.4). The selectivity index does not accurately represent the major diet

items, largely due to the plankton sampling protocol, which did not account for either insects or benthic zooplankton (i.e., harpacticoid copepods).

Interannual diet comparison

Overall, prey quantity of juvenile chum salmon was similar in 2003 and 2004. No significant differences ($P > 0.05$) were observed in the total mean weight or number of prey consumed (Table 1.1), %BW, or mean stomach fullness (Table 1.2) between years. However, juvenile chum salmon had a higher percentage of empty stomachs in 2003 (43%) than in 2004 (19%).

Diet composition varied both by number and weight between sampling years (Table 1.3; Figure 1.4). Numerically, diets consisted of small calanoids (60% and 48%), harpacticoids (8% and 16%), cyclopoids (7% and 1%), copepodites (2% and 13%), insects (8% and 16%), and other (12% and 7%) in 2003 and 2004, respectively. By weight, small calanoids and insects made up > 80% of the diet for both years, while other (17% and 5%) and harpacticoids (2% and 6%) made up only a small proportion of the diet in 2003 and 2004, respectively.

Patterns in numerical and gravimetric measures of diet composition were similar between years. Juvenile chum salmon consumed significantly greater %N of small calanoid and cyclopoid copepods, but significantly lower %N of harpacticoid copepods, copepodites, and insects in 2003 than in 2004 ($P = 0.011$ for insects; $P < 0.01$ for all other prey categories). Significantly lower %W of insects ($P < 0.001$) and copepodites ($P = 0.02$) were consumed in 2003 than in 2004, while no significant differences were observed for %W of small calanoids, harpacticoids, cyclopoids, and other between years.

Prey selection patterns also differed between years. In 2003, juvenile chum salmon feeding was opportunistic, with no significant selection values for any of the prey categories (Table 1.4). In 2004, significant ($P < 0.01$) positive selection was identified for small calanoids, while all other prey categories had no significant selection values. It should be noted that variance calculations could not be made for many of the prey

categories due to absence of a given prey category from either the plankton or the stomach samples.

Diet comparison by week

In 2004, prey consumption of juvenile chum salmon was compared for the 4 weekly sample periods spanning early May to early June. The mean number of prey per stomach increased from 109 ± 24.5 in week 1 (early May) to 226 ± 19.6 in week 4 (early June); however, mean prey numbers declined in week 2 ($\bar{x}$ = 28; S.E. = 6.4) and week 3 ($\bar{x}$ = 108; S.E. = 14.0) (Table 1.1). Juvenile chum salmon consumed significantly greater numbers of prey during week 4 than in weeks 2 and 3 (P = 0.001). Mean total weight of stomach contents also increased from week 1 to week 4, with week 4 fish having significantly greater stomach content weight than weeks 2 and 3 fish (P < 0.001). Mean %BW increased overall from 3.3 % in week 1 to 4.5% in week 4, although %BW dipped to 2.3 % in week 2. Mean %BW for weeks 1-3 were significantly (P < 0.05) lower than for week 4 (P < 0.05). Stomach fullness of juvenile chum salmon averaged 50% for all weeks sampled. The proportion of empty stomachs decreased from 28% in week 1 to 15% in week 4 (Table 1.2).

Diet composition also changed with sampling weeks in 2004. Generally, small calanoids, harpacticoids, copepodites, and insects were numerically the most important prey categories during each sampling week (Figure 1.5). Salmon consumed in week 4, a significantly higher (P < 0.001) proportion of small calanoid copepods than in any other week. At the same time, the contribution of harpacticoids declined by week. Juvenile chum salmon consumed a significantly greater (P < 0.001) proportion of harpacticoids during week 1 than weeks 2 and 4, while week 3 juveniles consumed a significantly greater (P < 0.001) proportion than week 4 juveniles. Insect diet percentages ranged from 27% to 13% for weeks 1 and 4. No significant differences were found for proportion of insects consumed between weeks.

The most important prey categories in terms of biomass were small calanoids and insects, although harpacticoids and other made up a small proportion of the diet during week 1 (Figure 1.5). Small calanoids increased in %W from week 1 (3%) to week 4 (52%), with significant difference between all weeks ($P < 0.05$ for weeks 1 and 2; $P < 0.01$ for all other weeks). Insects made up more than 50% of the overall diet biomass for all weeks, except week 4. Percent weight composition of insects did not differ significantly between weeks.

In 2004, prey selectivity varied between weeks (Table 1.4). Juvenile chum salmon had positive selection for small copepods in week 1 ($P < 0.01$) and week 4 ($P < 0.05$). Selection values for gammarid amphipods and isopods were slightly positive for weeks 1 and 4, respectively ($P < 0.01$).

Diet comparison by size class

Prey quantity varied with chum salmon size classes in both years. In 2003, the total mean number and weight of stomach contents increased with increasing size class (Table 1.1), although no significant differences were found. Juvenile chum salmon in the 50-59 mm size class fed at a significantly higher ($P < 0.01$) %BW than those in the 40-49 mm size class (Table 1.2). However, these larger juveniles had a lower feeding incidence (40%) than the 40-49 mm size class (45%; Table 1.2).

In 2004, total mean number of prey consumed increased from 65 (S.E. = 10.8) to 838 (S.E. = 79.7) for 30-39 mm and ≥60 mm fish (Table 1.1). Juvenile chum salmon of the smallest size class consumed significantly less prey than all other size classes ($P < 0.001$). Mean total prey weight also increased significantly with increasing size class ($P < 0.001$; Table 1.1). The 40-49 mm (4.1%) and ≥ 60 mm (4.6%) size classes had the highest average %BW (Table 1.2), but values were not significantly different ($P > 0.05$). Stomachs of juveniles 30-39 mm through 50-59 mm averaged 50% full, but juveniles ≥ 60 mm averaged 100% stomach fullness. Feeding incidence decreased with increasing size class (Table 1.2).

In both years of our study, prey composition varied between size classes both numerically and gravimetrically, but few significant differences were found. In 2003, the most important prey categories numerically were small calanoids followed by other, harpacticoids, and insects (Figure 1.6). For 2003, the only significant difference ($P < 0.01$) observed between the two size classes of chum was for harpacticoids, at 9 % for 40-49 mm fish versus 7 % for 50-59 mm juvenile chum salmon. Weight-based diet composition also varied with size. In 2003 and 2004, the most important prey categories in terms of biomass were small calanoids and insects (Figures 1.6 and 1.7). In 2003, small calanoids and insects combined made up $\geq 80\%$ of the average diet biomass for 40-49 mm and 50-59 mm juvenile chum salmon (Figure 1.6); however, no significant differences ($P = 0.05$) in composition were found between size classes.

In 2004, consumption of calanoids increased with increasing size class (Figure 1.7), with 30-39 mm juveniles consuming significantly ($P < 0.001$) lower numerical percentages than all other size classes. Conversely, significantly more ($P < 0.001$) harpacticoids were consumed by 30-39 mm juveniles than by all other size classes except the $\geq$60 mm size class (Figure 1.7). Insects were a numerically important part of the diet composition for 30-39 mm juveniles (19%), and less important for larger juveniles, but no significant differences ($P > 0.05$) were observed between size classes.

In 2004, the percent biomass of small calanoids increased with increasing size class from 21% to 97% (Figure 1.7). The smallest size class of chum salmon consumed significantly less %W of small calanoids than juveniles of all other size classes ($P < 0.001$). Conversely, the %W of insects decreased with increasing size class from an average of 55% to 3%, but the difference was not significant ($P > 0.05$).

In 2003 and 2004, chum salmon selected small copepods as prey, but fed on other prey opportunistically (Table 1.4).

Diet comparison by salinity range

The quantity of prey consumed by juvenile chum salmon varied with the salinity where they were captured, but the pattern was not consistent. The highest mean total

number (420 ± 52.2) and weight (0.045 g ± 0.005) of prey per gut were consumed by fish inhabiting the15-19 salinity range. Juvenile chum salmon in the 0-4 and 10-14 salinity ranges had significantly lower mean prey weights than juveniles in the 15-19 salinity range ($P < 0.001$). Fish in the 0-4 salinity range had the lowest mean number and weight of prey per stomach sampled (Table 1.1) and the highest proportion of empty stomachs (Table 1.2). Significantly more ($P < 0.001$) prey were consumed by fish in the middle 3 (5-19) salinity ranges than in the lowest range. Juveniles from the 5-9 and 15-19 salinity ranges had the highest mean %BW and stomach fullness (Table 1.2). However, mean %BW was significantly greater ($P > 0.01$) only for fish in the 5-9 salinity range compared to fish in the 0-4 or 10-14 ranges.

Numerically, juvenile chum salmon diet composition varied with salinity. Small calanoids composed the largest percentage of the diet in fish from the 10-14 and 15-19 salinity ranges, 90% and 87% N respectively (Figure 1.8). Fish sampled in the 10-14 salinity range consumed significantly more ($P < 0.01$) small calanoids than those in the 0-9, and 15-19 salinity ranges. Harpacticoids and insects composed the highest %N in stomachs from the 0-9 salinity ranges. The %N of harpacticoids consumed was significantly higher ($P < 0.01$) in the 0-4 salinity range than the 5-19 salinity ranges. Chum salmon juveniles in the 0-4 salinity range consumed a significantly higher ($P < 0.01$) %N of insects than juveniles in the 15-19 salinity range, and juveniles in the 5-9 salinity range consumed a significantly higher ($P < 0.01$) %N than juveniles in the 10-19 salinity ranges. Copepodites were most numerous in stomachs from the lowest and highest salinity ranges, 14% and 20% N respectively (Figure 1.8), but no significant differences were found.

Juvenile chum salmon diet also varied in %W with salinity. Gravimetrically the greatest prey categories were small calanoids and insects, although harpacticoids and other made up a small %W of the diet in the 0-4 salinity range (Figure 1.8). Stomachs sampled from the 15-19 salinity ranges had the highest %W of small calanoids. As a general trend, %W of small calanoids increased with salinity, with significantly higher ($P < 0.001$) %W's in stomachs from the 15-19 salinity range than stomachs from the 0-4 and

10-14 salinity ranges. Fish from the low salinity ranges, 0-4 and 5-9, had the highest %W of insects, 56% and 74% respectively. Generally, insects decreased in %W with salinity. The 0-4 salinity range contained a significantly greater ($P < 0.001$) mean weight of insects than stomachs from the 15-19 salinity range. In addition, juvenile chum salmon from the 5-9 salinity range had stomachs significantly greater in %W than those from the 10-14 ($P < 0.05$) and 15-19 ($P < 0.001$) salinity ranges.

Juvenile chum salmon prey selectivity varied according to salinity ranges (Table 1.4). Small copepods were positively selected for in all salinity ranges except the 0-4 salinity range ($P < 0.01$). Fish eggs had a positive selection value in the 20-29 salinity range ($P < 0.01$). No other prey categories had significant selection values (Table 1.4).

Diel feeding study

No patterns in diel feeding rhythm were detected. At a latitude as high as Kuskokwim Bay, there are only a few hours between sunset and sunrise, likely allowing insufficient time to detect differences in feeding success. Prey weight was highest in fish sampled between 1800 and 2300 hours, and lowest during the 0400 hour samples (Figure 1.9), but differences were not significant ($P = 0.067$).

DISCUSSION

Juvenile chum salmon diet in Kuskokwim Bay varied by size, season, salinity, and year, supporting the hypothesis that chum salmon during their estuarine early life stage are primarily opportunistic feeders (Healey 1982b). The main dietary items for juvenile chum salmon in Kuskokwim Bay were small calanoid and harpacticoid copepods and insects. These prey items have also been described as principal dietary components for juvenile chum salmon in other early marine studies throughout the North Pacific (Mason 1974, Bailey et al. 1975, Feller & Kaczynski 1975, Sibert 1979, Healey 1991, Sturdevant et al. 1996, Moulton 1997, Orsi et al. 2005).

While small calanoid copepods were commonly found in the diet of juvenile chum salmon captured in the 0-4 salinity range, these were predominately absent from concurrent plankton samples (Appendix C), possibly indicating that juvenile chum salmon were moving horizontally into waters of higher salinity and prey density to feed. Alternatively, juvenile chum salmon residing in low salinity/high turbidity water of the Kuskokwim River plume may rely on the tidal flow to provide them with a supply of small calanoid copepods and may have consumed these prey at an earlier time when they were present. Such dietary differences, due to tidal transport, in juvenile chum salmon were reported from Lymm Creek, British Columbia (Mason 1974).

During the earlier sampling weeks of 2004, the emigration of juvenile chum salmon had just started and fish were beginning to arriving in Kuskokwim Bay. Juvenile chum salmon entering estuaries tended to remain in areas of low salinity for up to a few days, gradually making the transition from freshwater to water of increasing salinity (Iwata & Komatsu 1984, Hillgruber et al. 2007). Early chum salmon juveniles might benefit from residing in the freshwater plume of Kuskokwim Bay, since the high turbidity of the river plume might shield them from predation. Similar mechanisms have been suggested for rainbow smelt (*Osmerus mordax*) in the St. Lawrence River estuary (Dauvin & Dodson 1990). In addition, residing in the lower salinity waters for extended periods may reduce metabolic costs associated with osmoregulatory changes. Alternatively, there may be disadvantages associated with residing in the high turbidity waters. For one, highly turbid waters receive less light penetration which may result in lower plankton abundances and fewer feeding opportunities. Secondly, visibility decreases and prey are more difficult to locate in turbid waters possibly leading to fewer prey encounters and lower feeding success (Utne 1997). Juvenile chum salmon in Kuskokwim Bay residing in the 0-4 salinity water displayed the lowest feeding success as was indicated by low feeding incidence and intensity.

Insects appeared to be more important to juvenile chum salmon in Kuskokwim Bay than has been reported for juvenile chum salmon in some other studies (Mason 1974, Feller & Kaczynski 1975, Healey 1979, Sibert 1979, reviewed by Salo 1991), particularly

in 2003. The highly turbid waters of upper Kuskokwim Bay may cause this high degree of dependence on drift insects. Highly turbid water has low light penetration, which inhibits marine productivity (Kelble et al. 2005) often resulting in surface oriented feeding. Juvenile chum salmon from Kotzebue Sound (reviewed by Salo 1991) and upper Cook Inlet (Moulton 1997), both turbid systems, were found to feed heavily on drift insects. Alternatively the large numbers of insect in the diet may be the result of juvenile chum salmon feeding in nearshore habitats with high insect productivity.

Harpacticoid copepods were most abundant in the diet of juvenile chum salmon sampled in low salinity (0-9) water. The main harpacticoid taxon found in the diet of juveniles was thought to be *Enhydrosoma sp.* (unpublished data), which is known to inhabit fresh to low salinity waters (Chris Stark, University of Alaska Fairbanks personal communication). Harpacticoids contributed less to the diet of Kuskokwim Bay juvenile chum salmon than previously reported (Feller & Kaczynski 1975, Sibert 1979, Higgs et al.1995). However, since the sampling protocol employed for this study did not include benthic sampling, the distribution and abundance of harpacticoid copepods cannot be assessed or compared with patterns of prey composition in juvenile chum salmon.

Feeding success (%BW) was higher for Kuskokwim Bay juveniles in both years (3.0%-3.8%) than chum salmon juveniles from the Columbia River (1%-2%; Morgan et al. 2005), and within the range found for chum salmon from Hecate Strait, British Columbia (2.9%-4.12%; Healey 1991). The most pronounced difference in diet between 2003 and 2004 was the higher proportion of empty stomachs from fish sampled in 2003, even though average stomach fullness and %BW were similar between years. These results may be an effect of a smaller sample size obtained in 2003 resulting in data that does not represent the overall juvenile population. Alternatively, prey density may have been reduced later in the season resulting in a drastic difference in feeding incidence among juveniles in 2003. It is noteworthy, however, that no other measure of juvenile feeding success (e.g., feeding intensity) differed significantly with sampling year. This might indicate that, in 2003, prey was more patchily distributed, resulting in a more variable feeding success for juvenile chum salmon.

Juvenile chum salmon from Kuskokwim Bay had a greater percentage of empty stomachs in both years of our study, (2003: 43%; 2004: 19%) than juveniles of a similar size from northern Cook Inlet (1.8%; Moulton 1997) and Hecate Strait British Columbia (0%-3.2%; Healey 1991). Average numerical feeding intensity was lower in Kuskokwim Bay (2003:116.8 prey/gut; 2004: 154.7 prey/gut) than for juvenile chum salmon of a similar size from Puget Sound (265.8 prey/gut; Feller & Kaczynski 1975), but higher than juveniles from Northern Cook Inlet (22.3 prey/gut; Moulton 1997). However, numerical feeding intensity by itself does not adequately reflect the energetic gain obtained; e.g., juvenile chum salmon from Northern Cook Inlet were feeding predominantly on drift insects and small copepods, similar in size to prey items ingested by chum salmon from Kuskokwim Bay.

In 2004, feeding intensity more than doubled from week 1 to week 4. This increase in the average number of prey per gut could be attributed to the higher water temperatures later in the season (Appendix B). As water temperature increases within the range of tolerable temperatures for fish, their metabolic rates and, thus, energetic costs also increase (Brett 1995). These increased energetic costs can only be met with increases in food supply.

Energy density was lower for juveniles entering the estuary later in the season (Hillgruber et al. 2007). A lower overall condition and higher proportion of empty stomachs may indicate a lower survival probability of juveniles migrating offshore later in the season. The larger juvenile chum salmon were feeding mostly on small copepods, since no large copepods were available in Kuskokwim Bay (Appendix C). Small copepods have a lower caloric value than insects (Griffiths 1977, Kosobokova 1980, Davis et al. 1998) or some large calanoid copepods, which might result in a lower growth rate or energetic loss of the piscine predator; however small calanoids are typically much more abundant.

The diel feeding rhythm results of Kuskokwim Bay juvenile chum salmon are comparable to results found from other studies (Willette et al. 1997). Juvenile salmonid feeding intensity generally increases after sun rise, remains steady during daylight hours,

and decreases after the sun sets. Kuskokwim Bay, being located at such high latitude, experiences long hours of daylight during the summer months, with only a few hours of darkness. Extended periods of daylight are likely the reason Kuskokwim Bay chum juveniles exhibit a steady feeding rate.

In conclusion, Kuskokwim Bay juvenile chum salmon fed on a similar prey spectrum as juvenile chum salmon from other systems. Although there was a higher dependence on drift insects than typically seen in juvenile chum salmon diets, this by itself does not indicate poor condition. However, chum salmon also had a lower than average feeding incidence than juvenile chum salmon from other studies, particularly in 2003, which might indicate a high proportion of fish feeding poorly, particularly those fish emigrating later in the season.

In this study, most juvenile chum salmon were caught in low salinity waters near the river mouth, possibly indicating an area of preference for the juvenile fish. However, concomitant plankton tows indicated that very little zooplankton was available in this low salinity water (Appendix C). This might indicate that juvenile chum salmon may either have been subject to suboptimal feeding conditions or that while fish were residing in the low salinity/high turbidity water, they were undertaking feeding excursions or relying on tidal transport to acquire prey.

The high percentage of empty stomachs found in Kuskokwim Bay juvenile chum salmon compared to juveniles from other systems should be noted. These results may indicate that zooplankton distributions vary interannually and might be patchy within the bay, possibly resulting in highly variable feeding success and mortality rates. Particularly smaller chum salmon juveniles entering the bay later in the season during times when water temperatures are elevated and metabolic rates consequently increased might experience reductions in energy density, growth, and possibly survival probability. Future research is necessary to further investigate the seasonal and annual differences in condition and survival potential for chum salmon during their estuarine residence in and migration through Kuskokwim Bay.

Table 1.1. Mean total weight and number of prey items per juvenile chum salmon stomach for year, size class (mm FL), salinity (2004), and week (2004). Standard errors are shown in parentheses. n = sample size, n/a = no samples available.

Year	n	Mean Total Prey Weight (g)	Mean Total Prey
2003	54	0.029 (0.003)	116.8 (23.7)
2004	311	0.026 (0.001)	154.7 (11.3)
Size Class			
2003			
30-39	n/a		
40-49	29	0.024 (0.003)	85.0 (22.2)
50-59	25	0.033 (0.004)	160.3 (43.7)
60-69	n/a		
2004			
30-39	89	0.011 (0.007)	65.2 (10.8)
40-49	156	0.027 (0.001)	133.5 (14.2)
50-59	63	0.042 (0.003)	215.2 (30.7)
60-69	3	0.085 (0.016)	838.3 (79.7)
Salinity			
0-4	187	0.021 (0.001)	93.1 (8.1)
5-9	41	0.043 (0.003)	210.6 (32.7)
10-14	27	0.033 (0.002)	247.3 (38.3)
15-19	35	0.045 (0.005)	420.2 (52.2)
20-29	4	0.017 (0.004)	71.8 (35.5)
Week			
1	38	0.012 (0.001)	109.0 (24.4)
2	36	0.011 (0.001)	28.1 (6.4)
3	90	0.021 (0.001)	108.0 (14.0)
4	147	0.037 (0.002)	226.4 (19.5)

Table 1.2. Percent body weight feeding rate (%BW), percent stomach fullness, and percent empty stomachs of juvenile chum salmon for years 2003 and 2004, size class, salinity range, and week. Values in parenthesis represent standard errors of the mean. n = sample size.

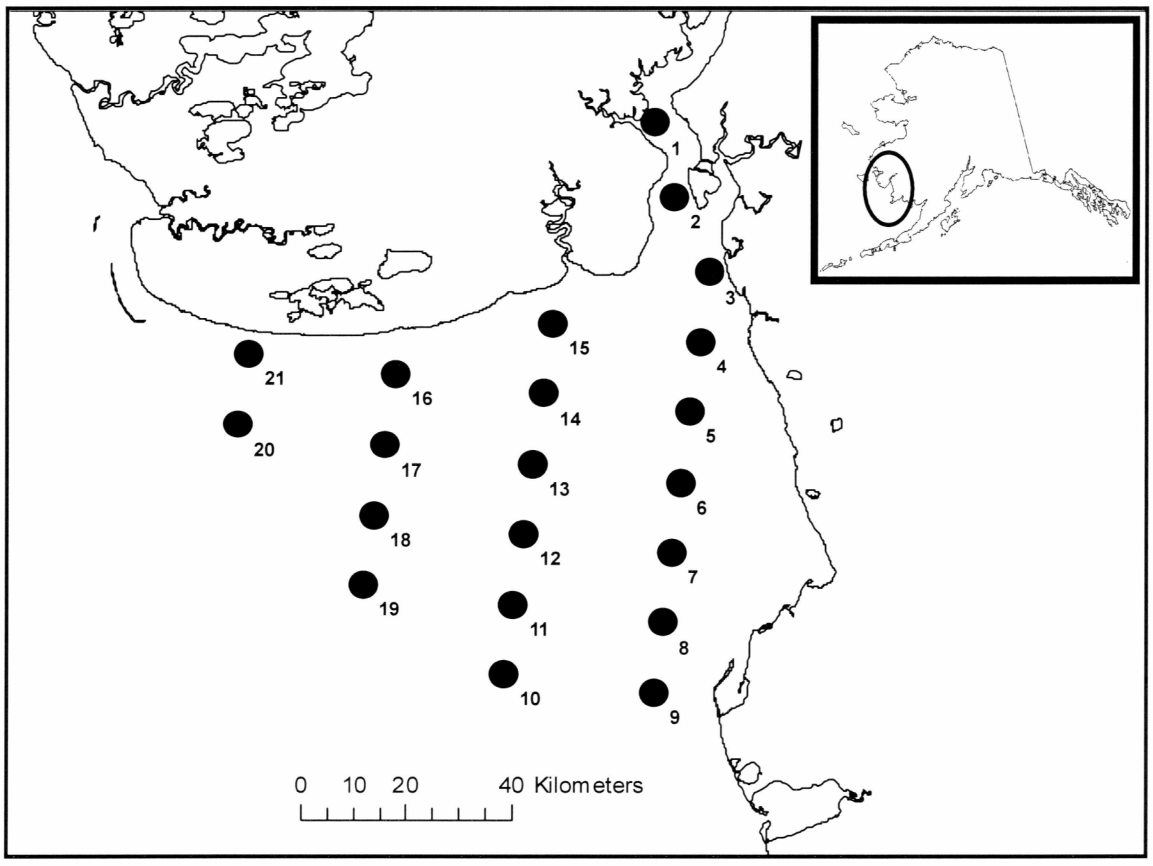
Year	n	%BW	%Fullness	%Empty Stomachs
2003	54	3.0 (0.003)	50	43
2004	358	3.8 (0.001)	50	19
Size class (mm)				
2003				
40-49	29	2.1 (0.003)	50	45
50-59	25	3.5 (0.005)	50	40
2004				
30-39	111	3.4 (0.002)	50	26
40-49	173	4.1 (0.002)	50	18
50-59	71	3.7 (0.002)	50	10
60-69	3	4.6 (0.013)	100	0
Salinity range				
0-4	231	3.5 (0.002)	50	26
5-9	41	5.5 (0.004)	75	0
10-14	28	3.5 (0.002)	50	4
15-19	35	4.6 (0.004)	75	0
20-29	4	3.1 (0.004)	50	0
Week				
1	46	3.3 (0.003)	50	28
2	38	2.3 (0.002)	50	26
3	108	3.4 (0.002)	50	19
4	166	4.5 (0.002)	50	15

Table 1.3. Average percent number (%N) and percent weight (%W) prey proportions, and percent frequency of occurrence (%FO) of major prey taxa from juvenile chum salmon diets for year, size class, salinity range, and week. Data were collected from Kuskokwim Bay, western Alaska. n = sample size.

		Calanoids <2.5mm			Harpacticoids			Cyclopoids			Copepodites			Insects			Other		
Year	**n**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**	**%N**	**%W**	**%FO**
2003	54	60%	39%	91%	8%	2%	57%	7%	0%	46%	2%	0%	50%	8%	42%	54%	12%	17%	34%
2004	311	48%	36%	83%	16%	6%	62%	1%	0%	20%	13%	3%	63%	16%	50%	60%	7%	5%	31%
Size Class (mm)																			
2003																			
40-49	29	63%	42%	97%	9%	10%	55%	6%	0%	10%	2%	0%	0%	5%	39%	45%	11%	17%	45%
50-59	25	58%	38%	84%	7%	7%	32%	8%	0%	24%	2%	0%	4%	11%	42%	60%	7%	10%	24%
2004																			
30-39	89	24%	21%	65%	25%	12%	66%	1%	1%	15%	19%	4%	56%	23%	55%	61%	**8%**	7%	28%
40-49	156	53%	39%	88%	13%	3%	65%	1%	0%	23%	12%	2%	69%	14%	51%	62%	7%	4%	31%
50-59	63	67%	47%	92%	10%	4%	52%	1%	0%	22%	6%	0%	68%	12%	43%	59%	4%	5%	37%
≥60	3	88%	97%	100%	0%	0%	0%	0%	0%	0%	11%	1%	100%	0%	3%	33%	0%	0%	0%
Salinity Range																			
0-4	187	33%	28%	78%	24%	9%	77%	1%	1%	20%	14%	2%	57%	20%	56%	63%	7%	4%	32%
5-9	41	68%	25%	90%	6%	1%	66%	1%	0%	49%	2%	0%	54%	22%	74%	90%	1%	1%	17%
10-14	27	90%	68%	100%	0%	0%	30%	0%	0%	11%	4%	0%	78%	1%	27%	48%	4%	5%	33%
15-19	35	87%	80%	100%	0%	0%	17%	0%	0%	3%	8%	0%	89%	1%	9%	23%	4%	10%	46%
20-29	4	44%	14%	75%	0%	0%	0%	0%	0%	0%	20%	0%	75%	4%	53%	75%	33%	33%	50%
Week																			
1	38	3%	3%	32%	36%	19%	71%	0%	0%	8%	21%	5%	50%	27%	62%	68%	13%	11%	42%
2	36	20%	17%	61%	15%	8%	47%	0%	0%	0%	34%	13%	78%	18%	50%	56%	13%	12%	42%
3	90	38%	32%	89%	21%	4%	79%	2%	1%	29%	16%	1%	66%	17%	59%	68%	6%	3%	26%
4	147	72%	52%	97%	8%	3%	53%	1%	0%	23%	3%	0%	62%	13%	42%	55%	4%	3%	29%

Table 1.4. Chesson's Selectivity Index (α) for year, size class (mm), salinity range, and week. Weeks 1-4 represent the sampling periods from 5/17-5/24, 5/25-5/31, 6/01-6/07, and 6/8-6/11. The index ranges from 1 (prey selection) to -1 (prey avoidance). Samples were collected from Kuskokwim Bay, western Alaska, 2004. Values in parenthesis represent the standard error. * and ** and bold type represent significance at the 0.05 and 0.01 confidence level. n = sample size.

Year	n	Fish larvae	Fish eggs	Copepods (<2.5mm)	Gammarids	Cladocerans	Ostracods	Mysids	Shrimp	Isopods	Bi-valves
2003	44	0.00	0.00	0.74 (0.017)**	0.00	0.05 (0.082)	0.00	0.00	0.00	0.00	0.2 (0.000)
2004	292	0.00	0.06 (0.276)	0.84 (0.016)	0.01 (0.000)	0.00 (3.950)	0.04 (1.340)	0.02 (0.586)	0.00 (0.000)	0.02 (0.398)	0.02 (0.519)
Size Class											
2003											
40-49	26	0.00	0.00	0.68 (0.000)*	0.00	0.05 (0.002)	0.00	0.00	0.00	0.00	0.27 (0.000)
50-59	17	0.00	0.00	0.82 (0.000)**	0.00	0.06 (0.000)	0.00	0.00	0.00	0.00	0.12
2004											
30-39	81	0.00	0.01 (0.004)	0.85 (0.000)**	0.02	0.00 (0.753)	0.05	0.06 (0.000)	0.00	0.00	0.02 (0.186)
40-49	147	0.00	0.05 (0.007)	0.85 (0.000)**	0.01 (2.175)	0.01 (0.517)	0.05	0.01 (0.055)	0.00 (0.000)	0.03 (0.206)	0.02 (1.483)
50-59	61	0.00	0.16 (0.008)	0.78 (0.001)	0.02	0.00	0.00	0.01 (19.946)	0.00 (0.000)	0.03 (0.163)	0.00
60-69	3	0.00	0.00	1.00 (0.000)**	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salinity Range											
0-4	173	0.00	0.00	0.86 (0.014)	0.02 (0.000)	0.01 (2.005)	0.04 (0.872)	0.04 (0.241)	0.00	0.03 (0.213)	0.02 (0.504)
5-9	39	0.00	0.00	1.00 (0.000)**	0.00	0.00	0.00	0.00	0.00	0.00	0.04 (10.196)
10-14	27	0.00	0.14	0.86 (0.000)**	0.00	0.00	0.00	0.00	0.00	0.00	0.000 (0.000)
15-19	35	0.00	0.40	0.60 (0.000)**	0.00	0.00	0.00	0.00	0.00 (0.000)	0.00	0.00
20-29	4	0.00	0.025 (0.000)**	0.75 (0.000)**	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Week											
1	33	0.00	0.03	0.76 (0.157)	0.03 (0.000)	0.00	0.06 (5.629)	0.12 (0.000)	0.00	0.00	0.06 (0.292)
2	33	0.00	0.06	0.82 (0.000)**	0.00	0.00	0.12 (0.000)	0.00	0.00	0.00 (0.000)	0.03 (1.083)
3	83	0.00	0.01 (0.000)	0.84 (0.015)	0.01 (0.000)	0.02 (2.895)	0.07 (0.334)	0.00 (0.000)	0.00	0.06 (0.419)	0.01 (1.752)
4	143	0.00	0.10 (0.000)	0.86 (0.001)	0.01 (0.000)	0.00	0.00	0.02 (1.858)	0.00 (0.000)	0.01 (0.000)	0.01 (5.325)



1.1. Kuskokwim Bay, western Alaska, sample area, and stations sampled for the 2003 and 2004 research cruises.

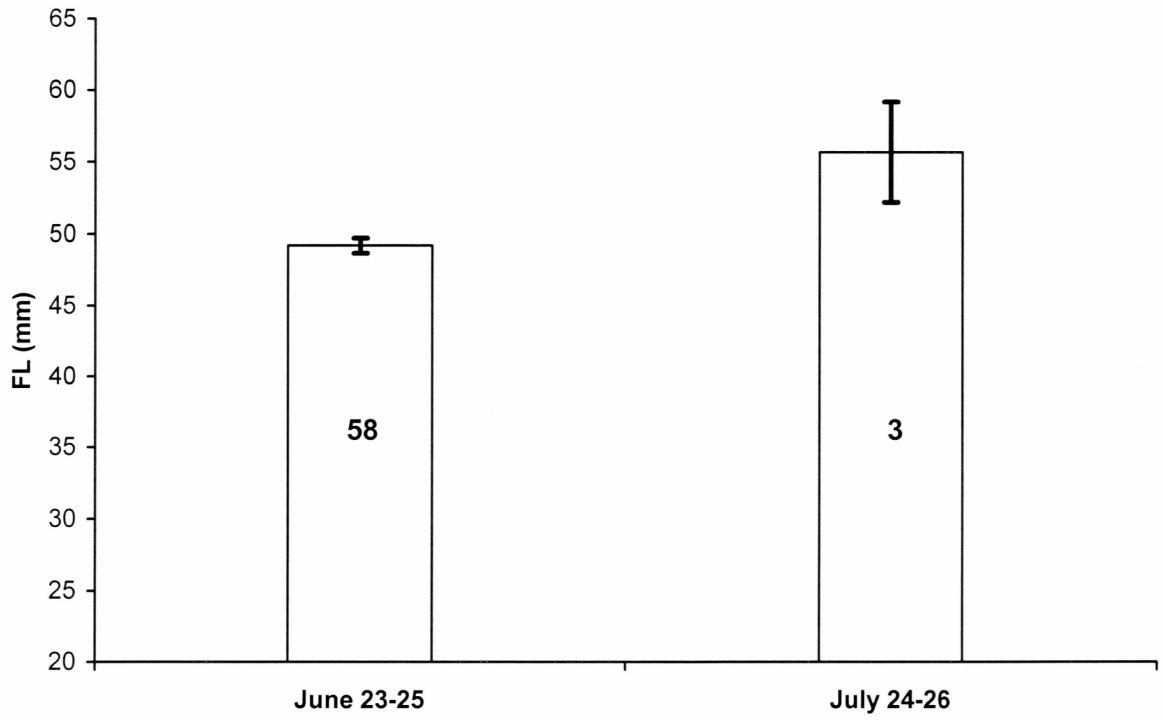


Figure 1.2. Mean fork length (FL), ± one standard error, of juvenile chum salmon sampled in Kuskokwim Bay, western Alaska, during cruises 1 and 2, 2003. Sample size shown in bars.

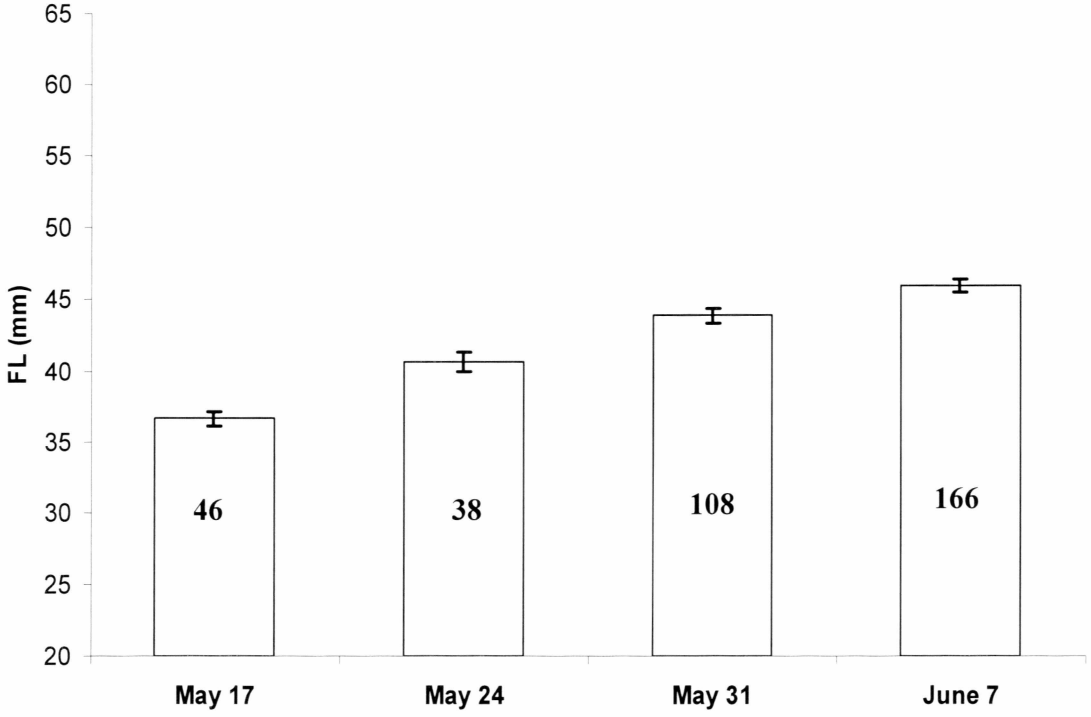


Figure 1.3. Mean fork length (FL), ± one standard error, of juvenile chum salmon in Kuskokwim Bay, western Alaska, during weeks 1-4, 2004. Sample size shown in bars.

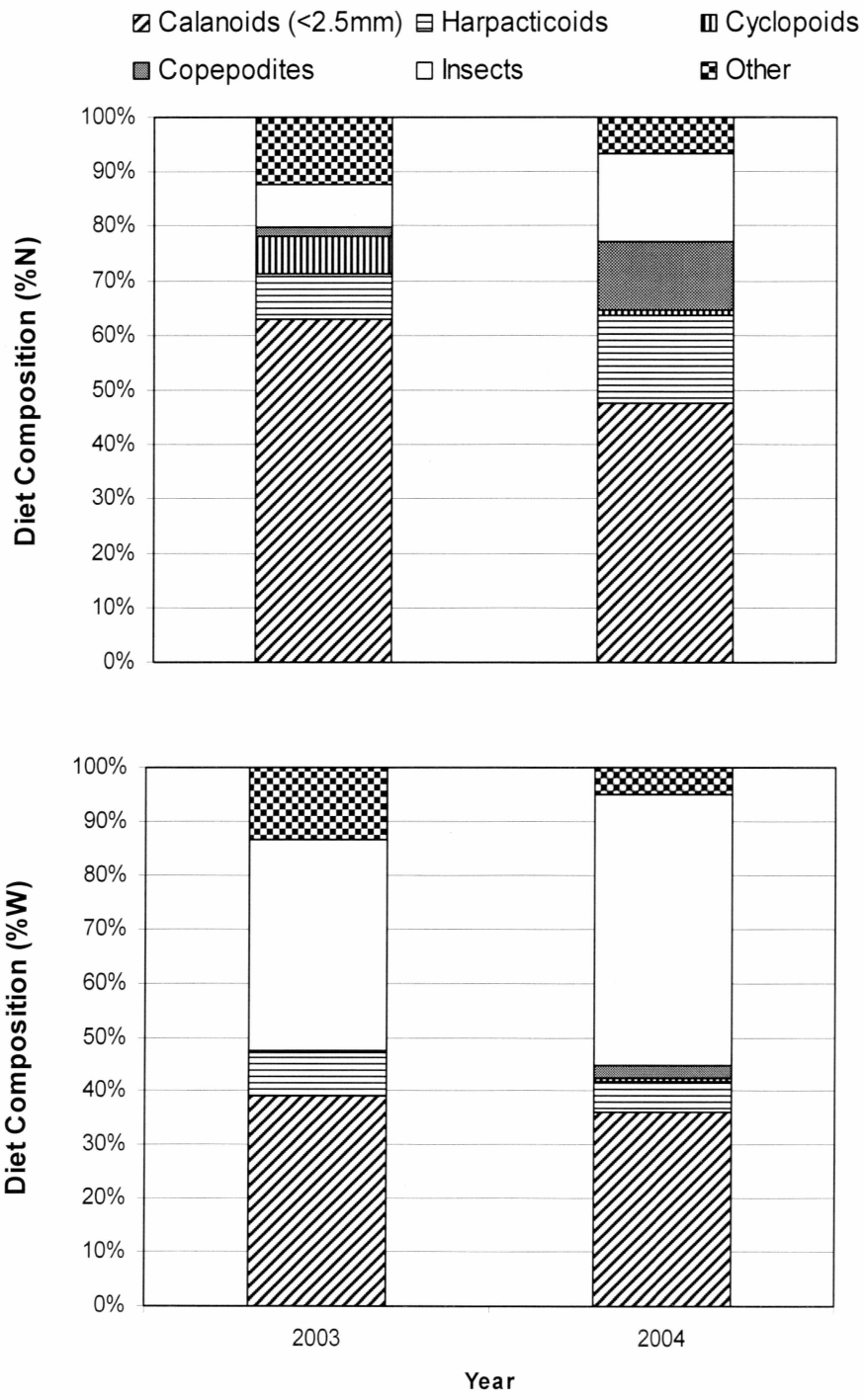


Figure 1.4. Prey composition as mean percent number (%N) and weight (%W) for sampling years 2003 and 2004 of juvenile chum salmon from Kuskokwim Bay, western Alaska. n = 31 and 290 for 2003 and 2004, respectively.

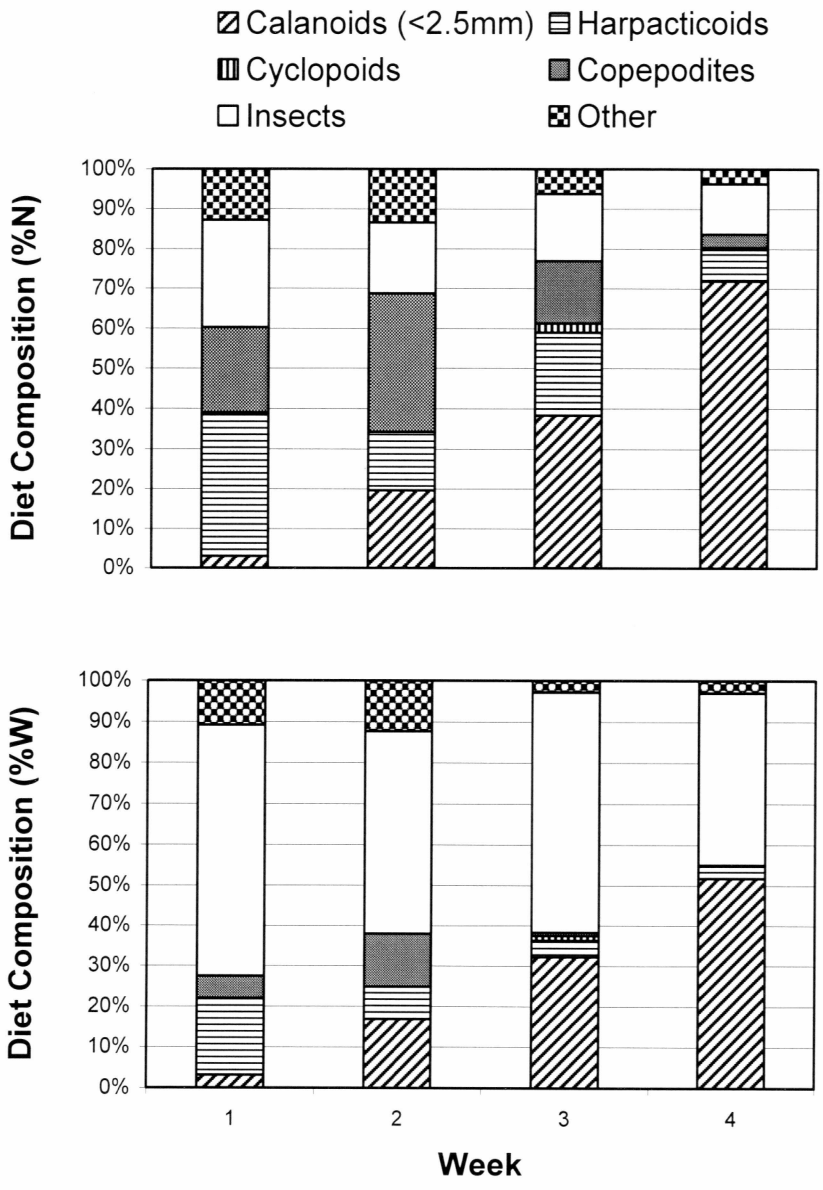


Figure 1.5. Prey composition shown as mean percent number (%N) and weight (%W) for sampling weeks 1-4 of juvenile chum salmon from Kuskokwim Bay, western, Alaska, 2004. Weeks 1-4 represent the sampling periods from May 17-24, May 25-31, June 1-7, and June 8-11. n = 38, 36, 90, and 147 for week 1-4 respectively.

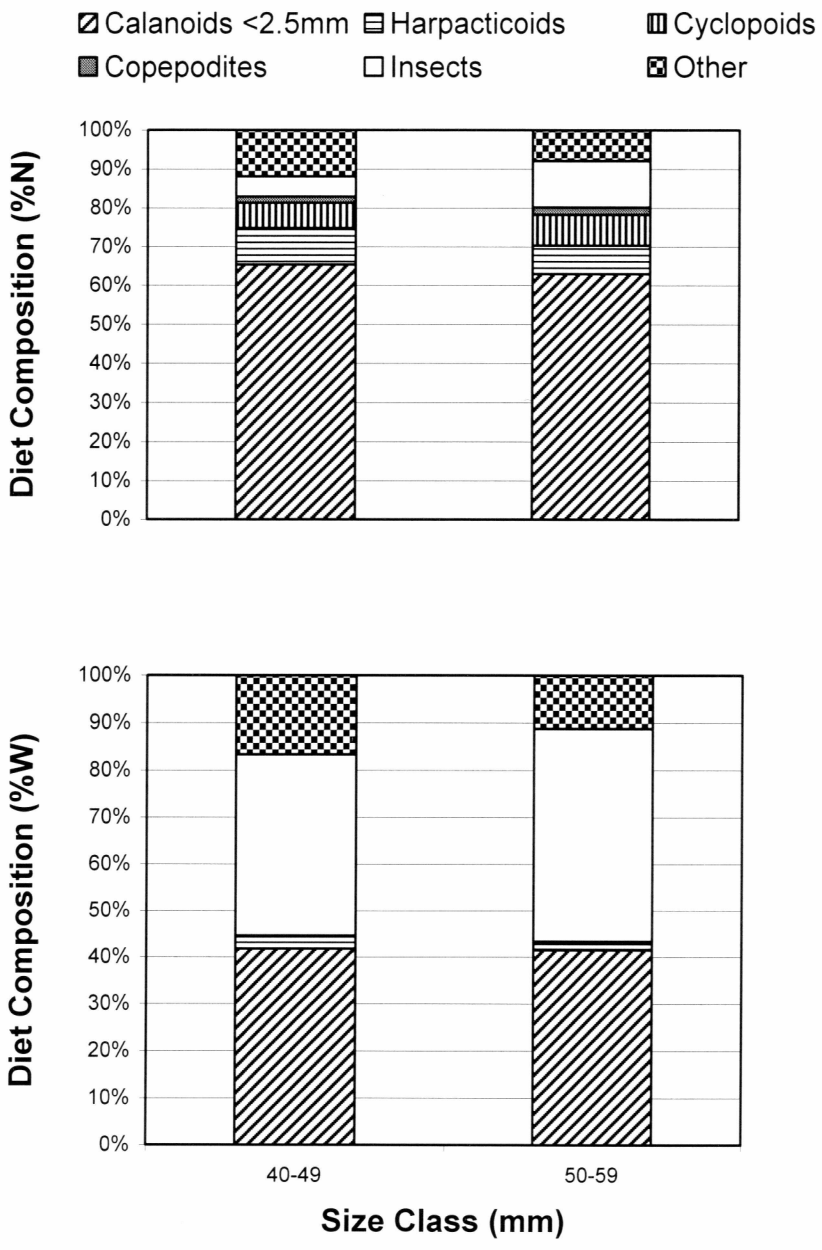


Figure 1.6. Prey composition shown as mean percent number (%N) and weight (%W) for size classes of juvenile chum salmon in Kuskokwim Bay, western Alaska, 2003. n = 26 and 17 for size classes 40-49 and 50-59 respectively.

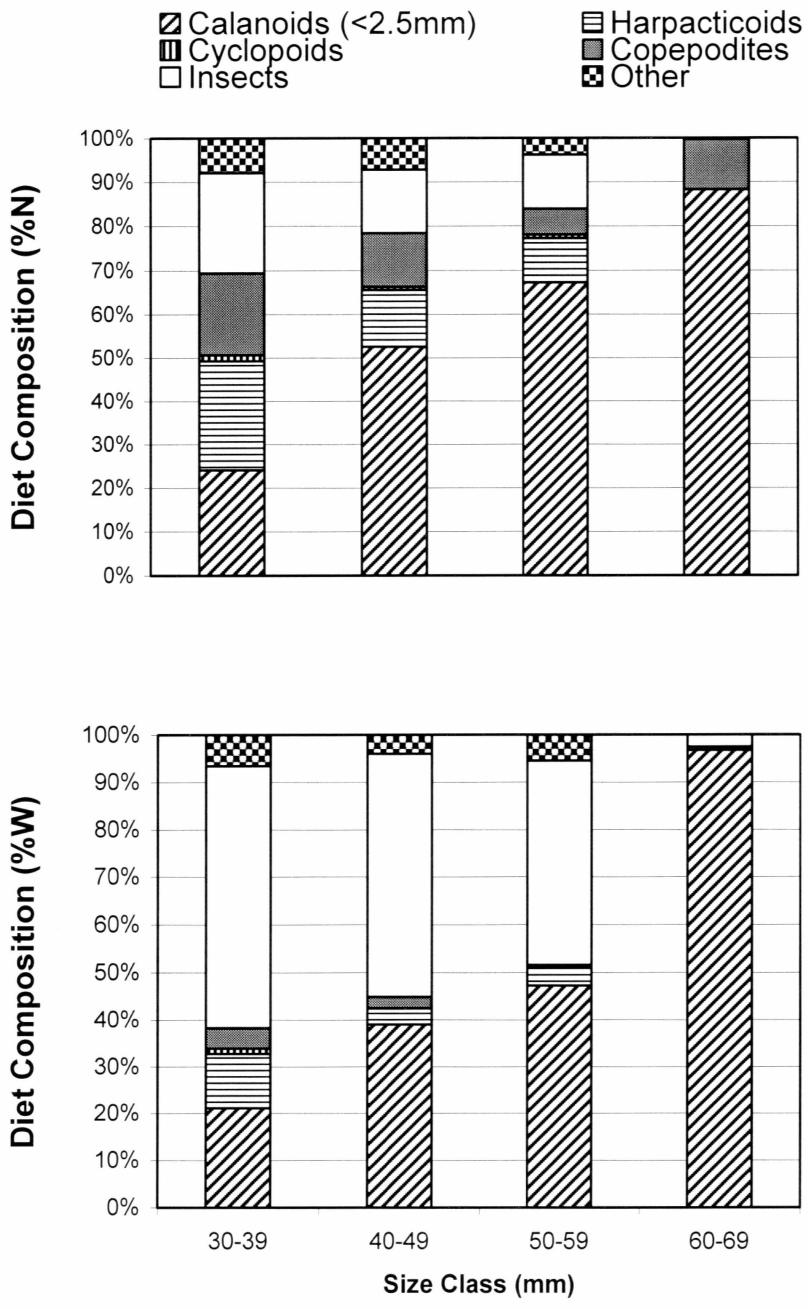


Figure 1.7. Prey composition as mean percent number (%N) and weight (%W) for size classes of juvenile chum salmon from Kuskokwim Bay, western Alaska, 2004. n = 89, 15, 63, and 3 for the 30-39 through 60-69 mm size classes, respectively.

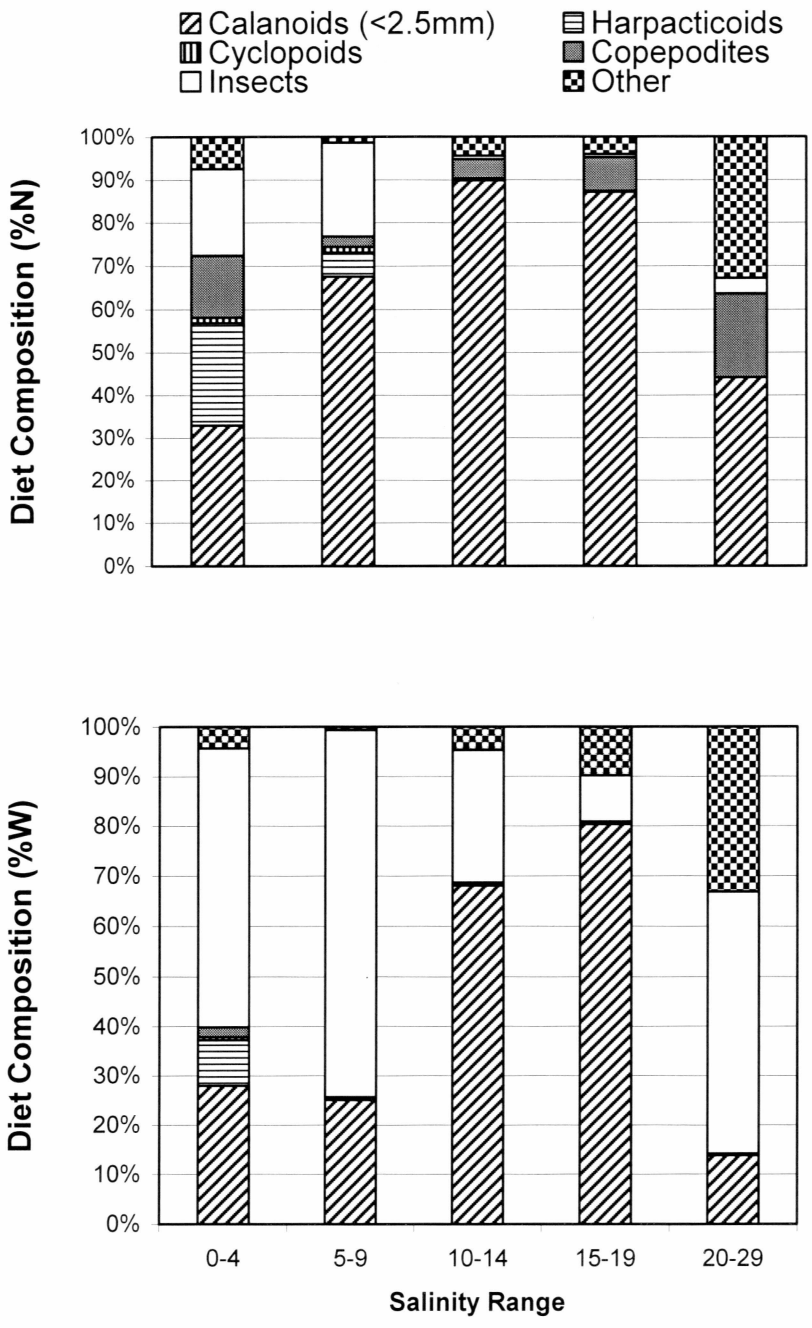


Figure 1.8. Prey composition as mean percent number (%N) and weight (%W) by salinity range of juvenile chum salmon from Kuskokwim Bay, western Alaska, 2004. n = 187, 41, 27, 35, and 4 for the 0-4 through 20-29 salinity ranges.

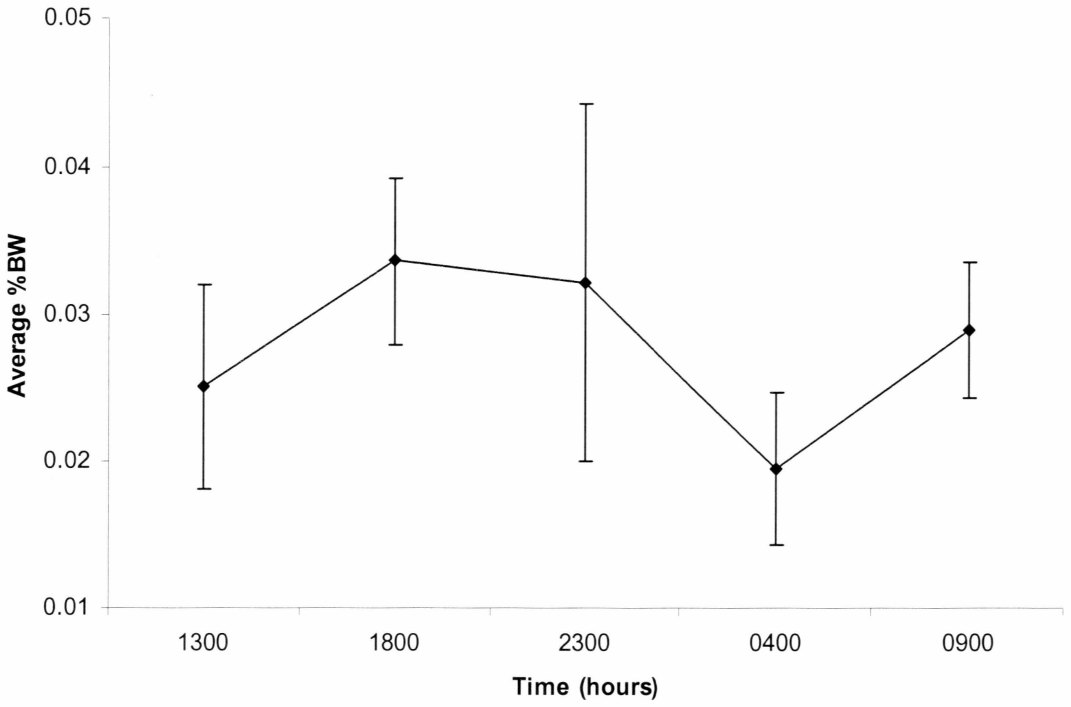


Figure 1.9. The relationship between time of day and the average amount of food in stomachs expressed as percent of wet body weight (%BW). Error bars represent ± 1 standard error about the mean. Sample sizes are 18, 25, 11, 13, and 21 for hours 1300-0900.

Appendix A. Percent numerical composition (%N) of all 25 prey taxa found in the diet of juvenile chum salmon in both 2003 and 2004 from Kuskokwim Bay, western Alaska. Bold type indicates values of one percent or greater.

Species	**2003**	**2004**
Calanoid copepods		
Tortanus spp.	0.52%	0.34%
Pseudocalanus spp.	-	0.63%
Eurytemora spp.	**64.27%**	**44.14%**
Acartia spp.	**13.62%**	**23.39%**
Harpacticoid copepods	**7.43%**	**13.17%**
Cyclopoid copepods	**7.65%**	0.69%
Copepodite copepods	**2.06%**	**11.58%**
Bivalve larvae	0.38%	0.02%
Fish eggs	0.03%	0.87%
Fish larvae	0.07%	0.00%
UNK. Crust	0.00%	0.49%
Gammarid amphipods	0.03%	0.01%
Isopods	0.00%	0.04%
Euphausiids	0.03%	-
Cladocerans	0.13%	0.11%
Ostracods	0.00%	0.11%
Shrimp	0.01%	0.05%
Mysids	0.00%	0.04%
Polycheates	0.00%	0.00%
Barnacle cypris	0.01%	0.00%
Echinoderm larvae	0.00%	0.00%
Nematodes	0.01%	0.09%
Insects	**3.74%**	**4.21%**
Chaetognaths	0.00%	0.00%
Cumaceans	-	0.01%

Appendix B. Year, cruise and station number, week, date, sampling time, tide level, sea surface temperature (SST), sea surface salinity (SSS), and sample size (n) for the 2003 and 2004 research cruises.

Year	Cruise	Station	week	Date	Time	Tide	SST	SSS	n
2003	1	1	-	6/23/2003	21:39	ebb	15	1	19
2003	1	2	-	6/24/2003	9:17	ebb	14	4	3
2003	1	X	-	6/24/2003	16:40	flood	-	-	6
2003	1	8	-	6/25/2003	10:45	ebb	14	16	1
2003	1	T1	-	6/25/2003	14:31	ebb	-	-	2
2003	1	T2	-	6/25/2003	16:03	flood	-	-	9
2003	1	T3	-	6/25/2003	17:57	flood	16	1	2
2003	1	T4	-	6/25/2003	19:50	flood	16	0	14
2003	2	1	-	7/24/2003	9:01	ebb	15	1	1
2003	2	12	-	7/26/2003	12:09	ebb	15	0	2
2004	1	1	1	5/17/2004	17:23	low slack	7	0	5
2004	1	2	1	5/18/2004	10:43	flood	6	0	6
2004	2	3	1	5/21/2004	13:48	high slack	8	2	2
2004	2	1	1	5/21/2004	16:30	ebb	9	0	2
2004	2	2	1	5/21/2004	19:30	low slack	9	0	2
2004	2	4	1	5/21/2004	21:58	flood	8	2	2
2004	3	5	1	5/24/2004	13:54	flood	8	14	1
2004	3	4	1	5/24/2004	15:17	high slack	9	6	4
2004	3	3	1	5/24/2004	16:48	ebb	9	3	3
2004	3	2	1	5/24/2004	18:20	ebb	10	0	4
2004	3	1	1	5/24/2004	20:09	ebb	10	0	15
2004	4	1	2	5/28/2004	10:20	ebb	12	0	13
2004	4	2	2	5/28/2004	12:22	ebb	-	-	15
2004	4	3	2	5/28/2004	14:20	flood	11	0	3
2004	4	6	2	5/29/2004	13:16	ebb	8	19	3
2004	4	7	2	5/29/2004	15:01	flood	8	23	2
2004	4	11	2	5/30/2004	12:28	ebb	7	26	2
2004	5	2	3	6/1/2004	11:11	ebb	12	0	15
2004	5	1	3	6/1/2004	12:45	ebb	12	0	25
2004	5	3	3	6/1/2004	13:42	ebb	-	-	4
2004	6	4	3	6/5/2004	12:00	flood	12	5	1
2004	6	20	3	6/5/2004	15:20	ebb	10	17	1
2004	6	3	3	6/6/2004	19:42	ebb	16	1	8
2004	6	1,1	3	6/7/2004	13:23	flood	14	0	18
2004	6	1,2	3	6/7/2004	18:20	ebb	14	0	25
2004	6	1,3	3	6/7/2004	23:21	flood	14	0	11
2004	6	1,4	4	6/8/2004	4:40	high slack	14	0	13

Year	Cruise	Station	week	Date	Time	Tide	SST	SSS	n
2004	6	2	4	6/8/2004	13:14	flood	14	0	21
2004	6	15	4	6/8/2004	17:54	ebb	12	18	19
2004	6	14	4	6/9/2004	7:30	ebb	11	19	12
2004	7	21	4	6/10/2004	14:13	flood	12	15	5
2004	7	20	4	6/10/2004	15:54	flood	12	13	20
2004	7	4	4	6/10/2004	18:06	high slack	13	7	11
2004	7	3	4	6/10/2004	19:23	ebb	14	3	17
2004	7	25	4	6/11/2004	12:26	ebb	13	5	22
2004	7	5	4	6/11/2004	14:23	flood	13	9	3
2004	7	26	4	6/11/2004	15:24	flood	12	12	2

Appendix C. Plankton abundances (numbers m^{-3}) by salinity range in Kuskokwim Bay for cruises 1 through 7, 2004. Only zooplankton present at a given salinity range were included. Bold type indicates numbers ≥1. Only salinities where juvenile chum salmon were caught are included.

		Cruise						
Salinity	**Plankton Taxa**	**1**	**2**	**3**	**4**	**5**	**6**	**7**
0-4	Fish larvae	0.26	0.03	0.00	0.00	0.01	0.04	0.00
	Fish eggs	0.00	0.05	0.00	0.00	0.20	0.00	0.00
	Copepods (>=2.5mm)	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Copepods (<2.5mm)	**1.28**	0.50	**1.06**	**4.14**	**5.07**	**10.12**	**27.88**
	Cladocerans	0.18	0.08	0.07	0.91	0.29	0.27	0.00
	Gammarid amphipods	0.01	0.06	0.00	0.00	0.00	0.00	0.02
	Ostracods	0.04	0.02	0.01	0.01	0.04	0.00	0.00
	Barnacle cyprid	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Unknown	0.51	0.24	0.05	0.00	0.01	0.00	0.00
	Polychaete Larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Polychaetes	0.01	0.00	0.00	0.01	0.03	0.01	0.00
	Mysiids	0.04	**2.90**	0.00	0.05	**2.58**	0.08	0.15
	Bivalve Larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Shrimp	0.00	0.00	0.00	0.00	0.03	0.00	0.00
	Isopods	0.02	0.00	0.00	0.36	0.07	0.00	0.00
5-9	Fish larvae			0.02			0.03	0.01
	Copepods (<2.5mm)			**75.36**			**8.03**	216.95
	Cladocerans			0.00			0.00	0.00
	Polychaete Larvae			0.04			0.00	0.00
	Mysiids			0.00			0.00	0.01
10-14	Fish larvae			0.05				0.04
	Fish eggs			0.00				**2.89**
	Copepods (<2.5mm)			**2100.57**				**707.50**
	Gammarid amphipods			0.00				0.00
	Echinoderm Larvae			0.00				0.72
	Unknown			0.00				0.01
	Polychaete Larvae			0.00				**2.32**
15-19	Fish larvae				0.00		0.08	
	Fish eggs				0.00		0.29	
	Copepods (<2.5mm)				**894.01**		**302.07**	
	Cladocerans				**4.51**		0.65	
	Gammarid amphipods				0.00		0.00	
	Barnacle cyprid				0.00		0.02	
	Echinoderm Larvae				0.00		0.24	

	Unknown	0.00	0.02
	Barnacle nauplii	0.00	0.13
	Polychaete Larvae	**6.01**	**9.55**
	Polychaetes	0.00	0.54
	Shrimp	0.00	**4.31**
	Hydrozoa/Scyphozoa	0.01	0.02
20-29	Fish larvae	0.02	
	Fish eggs	**14.47**	
	Copepods (<2.5mm)	**2.93**	
	Cladocerans	0.00	
	Gammarid amphipods	0.00	
	Barnacle cyprid	0.02	
	Echinoderm Larvae	0.01	
	Unknown	0.04	
	Barnacle nauplii	0.00	
	Polychaete Larvae	0.24	
	Crab Zoea	0.08	
	Hydrozoa/Scyphozoa	0.00	

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Patterns in energy density of juvenile chum salmon (*Oncorhynchus keta*) during estuarine residence in Kuskokwim Bay, Alaska[1]

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ABSTRACT: Chum salmon (*Oncorhynchus keta*) from Kuskokwim Bay, western Alaska were sampled in two years (2003 and 2004) to evaluate spatial and temporal patterns in their energetic content. Energy density was determined using bomb calorimetry and compared (1) interannually, (2) seasonally, (3) between juvenile size classes, and (4) between salinity ranges. In 2003, possibly due to low catches of juvenile chum salmon, no significant differences in energy density were found. In 2004, energy density decreased significantly from 5,371 cal g^{-1} in mid-May to 4,932 cal g^{-1} in mid-June. As juvenile chum salmon increased in size, their energy density significantly decreased. In addition, a seasonal decrease in energy densities from May to June was apparent in all size classes, except in the largest, those ≥60 mm. Energy density differed significantly between salinity ranges, but no clear pattern was apparent. The decrease in fish energy content with season and size suggests that juvenile chum salmon were allocating the majority of their energy towards growth and smoltification, rather than lipid storage. However, the significantly lower energy content of similar sized chum salmon outmigrating into the bay in June versus in May might be the result of higher metabolic costs, related to higher sea surface temperatures later in the season. If seasonally increasing energy demands, are not balanced by an increasing food supply, the severe implications potentially include declines in growth rates and possibly overall survival probability of chum salmon juveniles in Kuskokwim Bay.

KEY WORDS: Energy density, Chum salmon, Estuary, Kuskokwim Bay

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INTRODUCTION

Fish use a variety of energetic strategies to maximize their condition and their growth potential throughout their lives (Jobling 1994, Brett 1995). An increase in a fishes energy density indicates an increase in lipid storage for reproduction and or protein synthesis for growth. Generally, the energy density of fish increases with increasing fish size (Stewart et al. 1983, Lawson et al. 1998, Paul & Paul 1998, Trudel et al. 2005, Tirreli et al. 2006), and may vary interannually, seasonally, or as the result of physiological changes such as metamorphosis, smoltification or reproductive maturity of the fish (Montevecchi & Piatt 1984, Anthony et al. 2000). In Pacific salmon, juveniles undergo energetically costly physiological changes as they adjust to marine water during the estuarine outmigration (Iwata & Komatsu 1984). Condition and growth of juveniles during the early estuarine life stages are thought to be important factors in determining overall marine survival success (Parker 1971, Holtby et al. 1990).

Environmental factors such as water temperature can have dramatic impacts on growth rates of juvenile Pacific salmon. Water temperature is a major factor in regulating metabolic rates in ectothermic animals such as fishes (Brett 1995) and controls the rate of biochemical reactions, potentially causing fluctuation in metabolic rate (Fry 1971, Jobling 1994). As water temperature increases within the range of tolerable temperatures for fish, their metabolic rates increase along with energetic costs. These increased energetic costs can only be met with increases in food supply or decreased activity. While maximum growth potential for juvenile sockeye salmon (*Oncorhynchus nerka*) was determined at 15˚C, it was noted that maximum growth rates could only be achieved with adequate food availability (Brett 1995).

Zooplankton abundance and distribution is often patchy and dependent on environmental variables such as water temperature and salinity, as well as phytoplankton abundance (Cooney et al. 2001). In addition, caloric content of zooplankton can vary greatly with taxonomic group, seasonally, and spatially (Costa et al. 2006). Consequently, the diet composition of juvenile salmon may be an important factor in understanding energetic requirements and their effects on maximizing growth and survival in fish (Cho

1983, Higgs et al. 1995). For example, an energetics study on juvenile chum salmon (*O. keta*) in Washington estuaries, found prey energy levels to peak in early March and then decline through the remainder of the outmigration of chum salmon (Wissmar & Simenstad 1988); this decline in energy content of the food supply is likely to have an effect on growth and thus survival probability of juveniles passing through the estuaries later in the season. Maximizing growth is especially important for chum and pink salmon (*O. gorbuscha*), since they enter estuaries at a very small size, and are highly susceptible to size-selective mortality (Parker 1971, Simenstad & Salo 1980, Healy 1982b, Simenstad & Wissmar 1984, Hargreaves & LeBrasseur 1985, Moss et al. 2005). Thus, understanding energy allocation in these species might provide insight into patterns of growth and survival during their estuarine residence.

Chum salmon from the Kuskokwim River have experienced low escapement numbers over the last decade; and to date, the reasons for these low returns are unknown (ADF&G 2000). However, since only little information is available on the ecology of chum salmon from Kuskokwim River and even less on the early estuarine ecology of juvenile chum salmon in Kuskokwim Bay, it is difficult to assess the validity of hypotheses regarding population regulation of chum salmon in this watershed. Poor condition and inadequate growth of Kuskokwim Bay chum salmon juveniles may be contributing to poor marine survival and ultimately affecting stock abundance. The energy density of juvenile salmonids can be viewed as an index of their overall condition, thus allowing the assessment of the productivity of their estuarine rearing habitat.

The overall goal of this study is to evaluate patterns in energy density of chum salmon juveniles during their estuarine residence in Kuskokwim Bay. Specifically, juvenile chum salmon from Kuskokwim Bay were examined for differences in energy content (1) by year, (2) within and between sampling months, (3) between juvenile size classes, and (4) between salinity ranges. A better knowledge of condition patterns and energetic trends may improve our understanding of the importance of the estuarine residence for chum salmon juveniles, and may allow an evaluation of factors responsible

for year-class strength in Kuskokwim River chum salmon stocks as well as comparisons to other systems.

METHODS AND MATERIALS

Field Methods

This study was conducted in Kuskokwim Bay, a large, shallow bay in western Alaska (Figure 2.1). Large parts of Kuskokwim Bay are extremely shallow, with depths between 2 and 6 m. Kuskokwim Bay provides migration and possibly nursery habitat for five species of Pacific salmon, namely pink, chum, sockeye, coho (*O. kisutch*) and Chinook salmon (*O. tshawytscha*).

Samples were collected in two years, aboard the S/V 'Eileen O'Farrel' in 2003 and the F/V 'Namorada' in 2004. All samples were collected on a spatial grid of 22 stations. In 2003, sampling was conducted during three research cruises, June 23-25, July 24-26 and August 26-30 (Appendix A). In 2004 sampling began May 17 and continued until June 11. At each station, hydrographic data were collected with a SeaBird Electronics SBE-19 Seacat Conductivity-Salinity-Depth (CTD) profiler.

Fish sampling was conducted during daylight hours with a modified Kvichak trawl (3.1 m height x 6.1 m width x 15.0 m length). The Kvichak trawl, traditionally fished between two boats, was equipped with two doors to provide horizontal spread for the net. Floats at the headrope and weights at the footrope provided vertical spread and assured that the net fished at the surface.

After recovery of the trawl, all collected fish were anesthetized in MS-222 prior to handling. Fish treatment followed a protocol approved by the University of Alaska Fairbanks Animal Care and Use Committee (IACUC # 03-18). All fish were identified to species and counted if the total catch was less than 500 fish. The total catch was weighed if in excess of 500 fish. All chum salmon juveniles were measured for both standard (SL) and fork length (FL) to the nearest 1 mm and frozen.

Laboratory Methods

Juvenile chum salmon were sorted into 10 mm size classes, namely 30-39 mm, 40-49 mm, 50-59 mm, and ≥ 60 mm FL. Ten individuals from each size class were selected for both, analyses of diet (Chapter 1) and energy density. Wet weight of each fish was measured to the nearest 0.001 g. Gill rakers on the first gill arch were counted to confirm species identification. Both saggital otoliths were removed for later analysis of age and microchemistry. The stomachs were removed and all prey were carefully emptied and fixed in 10% formalin tapwater solution. The empty stomach and viscera were returned into the body cavity for analysis of whole body energy content. Whole fish weight minus otoliths and stomach contents was measured to the nearest 0.001 g wet weight (WW). Processed fish were placed in whirl-pak bags and stored in a freezer at -27 ºC for later processing. Prior to bomb calorimetry, the frozen juveniles were placed in a freeze dryer (VirTis, Freezemobile 12) at -60 °C until weight stabilized, confirming minimal moisture content of the sample; dry weight (DW) was recorded to the nearest 0.001 g. Each individual was homogenized with a mortar and pestle, and a ≤0.150 g pellet was pressed from a sub-sample of the homogenate and weighed immediately. For juvenile chum salmon less than 0.150 g all body tissue homogenate was used in the pellet. A semimicro Parr 1425 calorimeter was used to measure caloric content. Methods used for bomb calorimetry closely followed the Parr manual (Parr Instrument Co. 1994). Sulfuric and nitric acid formation was disregarded in calculations used for energy density because they are considered insignificant (Parr Instrument Co. 1994).

Statistical Methods

A two-factor analysis of variance (ANOVA) was used to compare energy density by sampling month, size class, and salinity range. A two sample t-test was used to compare energy density between years. Normal probability plots and one-sample Kolmogorov Smirnoff tests were used to test for normality of the data. Scheffe's multiple comparison tests were used to examine pairwise relationships if significant differences were detected. Since fish length (size class) was a covariate with month and salinity

range, fork length was regressed against energy density, and the resulting residuals were used for ANOVA to test for differences in energy density of juvenile chum salmon by month and salinity range. Linear regressions were conducted to assess the relationships between juvenile chum salmon energy content and FL (raw and log-transformed), %DW, and log-transformed DW.

RESULTS

General

The energy density of 350 juvenile chum salmon was analyzed, including 59 fish from 2003 and 291 fish from 2004. Fish size ranged from 42-65 mm FL (mean = 49 mm, SD = 3.30) in 2003 and from 31-66 mm FL (mean = 44 mm, SD = 6.00) in 2004. Fish weight ranged from 0.55-2.47 g WW and 0.04-0.68 g DW in 2003 and from 0.17-2.36 g WW and 0.03-0.51 g DW in 2004.

In 2003 and 2004, dry weight was a function of fish length (Figure 2.2). The regressions for both years were:

2003: $\log (DW)\ [g] = 2.2892 \cdot \log (FL) - 12.944 \quad r^2 = 0.7939;\ n = 59$

2004: $\log (DW)\ [g] = 3.7235 \cdot \log (FL) - 16.167 \quad r^2 = 0.9532;\ n = 291$

Monthly Comparisons

Energy density of juvenile chum salmon generally declined over the season (Figure 2.3). In 2003, mean energy densities decreased slightly from 4,751 to 4,709 cal g^{-1} DW in late-June to late-July, but the difference was not significant between sampling months. By comparison, in 2004, mean energy density decreased significantly, from 5,371 to 4,932 cal g^{-1} between mid-May and mid-June (ANOVA; $F = 26.959$, $df = 287$, $P < 0.001$); differences were significant between all periods except early and mid-June ($P \leq 0.002$). In the same time interval, average sea surface temperature (SST) in Kuskokwim Bay increased from 7 °C in May to 15°C in July (Figure 2.3), with the biggest change between mid-May and early-June.

Size Class Comparisons

Energy density varied with juvenile chum salmon size class in both years, but the pattern was different (Figure 2.4). In 2003, energy density increased from 4,724 to 4,862 cal g^{-1} DW for juveniles in the 40-49 mm and ≥60 mm size classes, but the differences were not significant (T-test, $P > 0.05$). In 2004, energy density decreased significantly with increasing size class (ANOVA; $F = 36.873$, $df = 287$, $P < 0.001$). Juvenile chum salmon in the 30-39 mm FL range had significantly greater energy density than all other size classes ($P < 0.001$), except the ≥ 60 mm FL class ($P = 0.055$). In addition, energy density of juvenile chum salmon in the same size class differed between sampling months (Figure 2.5), and was significantly greater in May than in June for the 30-39 mm ($P < 0.001$), 40-49 mm ($P < 0.001$), and 50-59 mm ($P < 0.01$) size classes.

No significant relationship was found between energy density and FL for both years (Figure 2.6). Energy density and %DW were not related in 2003 ($r^2 = 0.01$) or 2004 ($r^2 = 0.03$).

Salinity Range Comparisons

In 2003, all chum salmon juveniles were captured within the 0-5 salinity range. Therefore, no patterns of energy density with regard to salinity could be examined for this year. In 2004, energy density of fish sampled at different salinities varied significantly (ANOVA; $F = 4.416$, $df = 268$, $P < 0.01$; Figure 2.7). Energy density was greatest for juvenile chum salmon collected in the 0-4 salinity range (5,060 cal g^{-1} DW). However, only juveniles sampled from the15-19 salinity range had significantly lower energy densities ($P < 0.05$).

DISCUSSION

Energy density decreased with increasing FL of juvenile chum salmon and with season in Kuskokwim Bay. These results differ from most studies, which generally

demonstrate an increase in energy density with increasing fish length (Stewart et al. 1983, Lawson et al. 1998, Paul et al. 1998, Trudel et al. 2005, Tirelli et al. 2006) and season. A poor correlation between energy density and %DW is an indication that Kuskokwim Bay juvenile chum salmon have different energy expenditures than do juvenile coho and Chinook salmon; percent dry mass was found to be strongly correlated with energy density in juvenile coho and Chinook salmon (Trudel et al. 2005). However, some studies on juvenile chum salmon report similar findings of a decrease in energy density with increasing FL (Orsi et al. 2004, Sturdevant et al. 2006).

Energy density of juvenile chum salmon was similar to those values observed for juvenile chum salmon of a similar size in Icy Strait Southeast, Alaska (Orsi et al. 2004); however, average SST was higher in Kuskokwim Bay than in Icy Strait. Juvenile chum salmon of similar size entering Kuskokwim Bay in May had higher energy density than those entering the bay in June. One possible explanation for this difference in condition is the increased water temperatures in June compared to May (Figure 2.3; Chapter 1, Appendix A). As waters temperatures increase, so do the metabolic rates of ectothermic fish such as salmon, causing energy reserves to be used at a higher rate (Brett et al. 1969, Brett 1995). However, metabolic costs are also lower with more isotonic water conditions (Jobling 1974), and salinity was higher in mid mid-May than in early-June. Energy density has been found to be closely correlated with % lipid content in juvenile salmonids (Brett 1995, Trudel et al. 2005). Unless enough food is consumed to satisfy the increased metabolic demand, juvenile energy density and growth rate will decline. Kuskokwim Bay juvenile chum salmon fed at a higher percent body weight per day during June than May (Chapter 1, Table 1.2), suggesting temperature as a major factor responsible for lower energy densities in June.

Prey type, due to varying chemical make-up, can have an impact on the energetics of salmonids (Cho 1983, Higgs et al. 1995). Kuskokwim Bay juveniles fed almost entirely on small copepods and insects in 2003 and 2004 (Chapter 1, Table 1.3). In May of 2004, insects made up a greater portion of the diet than in June. Insects have a higher energy density (4,532 J g^{-1} wet wt) than small calanoids (3,811 J g^{-1} wet wt) (Griffiths

1977, Kosobokova 1980, Davis et al. 1998). Thus, switching from a diet composed of small copepods and insects to a diet dominated by mostly small copepods may have decreased the energetic gain for juvenile chum salmon. In addition, elevated water temperatures in June will have resulted in higher metabolic rates, which could explain the observed decrease in energy densities in juvenile chum salmon from May to June.

Juvenile chum salmon of Kuskokwim Bay origin that were caught along the southern Bering Sea shelf in August-October of 2002 averaged 188 mm FL (Farley et al. 2005), indicating that juveniles more than doubled in size from early July to August-October in 2003. In addition, these surviving juveniles had greater energy densities (4,998 cal g^{-1} DW) than the juvenile chum salmon preparing to leave Kuskokwim Bay in mid to late June and July, thus after leaving Kuskokwim Bay, juvenile chum salmon seem to undergo a change in energy allocation resulting in an increase of condition with increasing size. However, it should be noted that juvenile chum salmon sampled in the Bering Sea surveys are not necessarily the same fish as those observed in Kuskokwim Bay in June and July.

Although very few studies have examined the energy density of juvenile chum salmon residing in estuaries, energetic strategies are likely to be different for juvenile chum salmon than for other Pacific salmon species, with the exception of pink salmon because these juvenile salmon enter the marine environment at a smaller size. High growth rates will shorten the period of increased vulnerability to size selective mortality and the physiological stress of osmoregulatory changes will further increase the energetic demands on the outmigrating juvenile fish. Apparently smaller juveniles have higher energy densities than larger juveniles, which is likely the result of residual yolk reserves. This is also confirmed by results from the microchemistry analysis of the juvenile chum salmon otoliths (Hillgruber et al. 2007). The Sr/Ca ratio of chum salmon of the smallest size classes still had a marine signature, indicating the maternal influence on the juvenile nutrition. However, residual lipid reserves appear to be quickly allocated towards somatic growth. Since 1 g of lipid has almost twice the caloric value of 1 g of protein, the outcome is an overall lower energy density with increasing size. We suspect that the

caloric value of prey is lower for later larger juveniles that switch to a diet strictly of small calanoids (Chapter 1, Table 1.3). Furthermore, as water temperature increases with season, the metabolic rates and thus the rate at which lipid reserves are utilized also increase. Therefore even though they are similar in size, fish entering the estuary later rather than earlier in the season have lower energy densities. In addition, a higher number of empty stomachs were found in juveniles entering the bay later in the season (Chapter 1, Table 1.2), which might further deteriorate the condition of the outmigrating chum salmon juveniles.

Following the reasoning of the match-mismatch hypothesis (Cushing 1990), which suggests that the degree of overlap of fish larvae and their prey affects larval growth, survival and recruitment, juvenile chum salmon outmigrating later in the year after the main plankton bloom will likely suffer reduced growth rates and an accompanied higher likelihood of mortality. Therefore, the match-mismatch hypothesis may play a major role in the over all recruitment success of juvenile chum salmon while rearing in Kuskokwim Bay.

Large calanoid copepods, which constituted a major part of juvenile chum salmon diet in other studies (Healey 1991, Willette et al. 1997), were absent from the plankton in Kuskokwim Bay (Hillgruber et al. 2007). The less energetically valuable small calanoids that constitute the majority of the plankton community in Kuskokwim Bay may be providing an energetically less valuable food source, ultimately limiting growth rates of juvenile chum salmon while in the bay.

No information exists about the possible population structure outmigrating cohorts of chum salmon juveniles in Kuskokwim Bay. If the sequence/pattern of outmigration timing is a function of chum salmon population structure, then it is likely that different smolt cohorts will experience differences in condition, growth, and likely survival probability. Future research in Kuskokwim Bay should further examine seasonal patterns in condition, growth, and mortality rates of different chum salmon cohorts. In addition, a better understanding of Kuskokwim River chum salmon populations is necessary to elucidate the effects of changing environmental conditions on differential

survival probabilities of chum salmon smolts during their estuarine residence in Kuskokwim Bay, Alaska.

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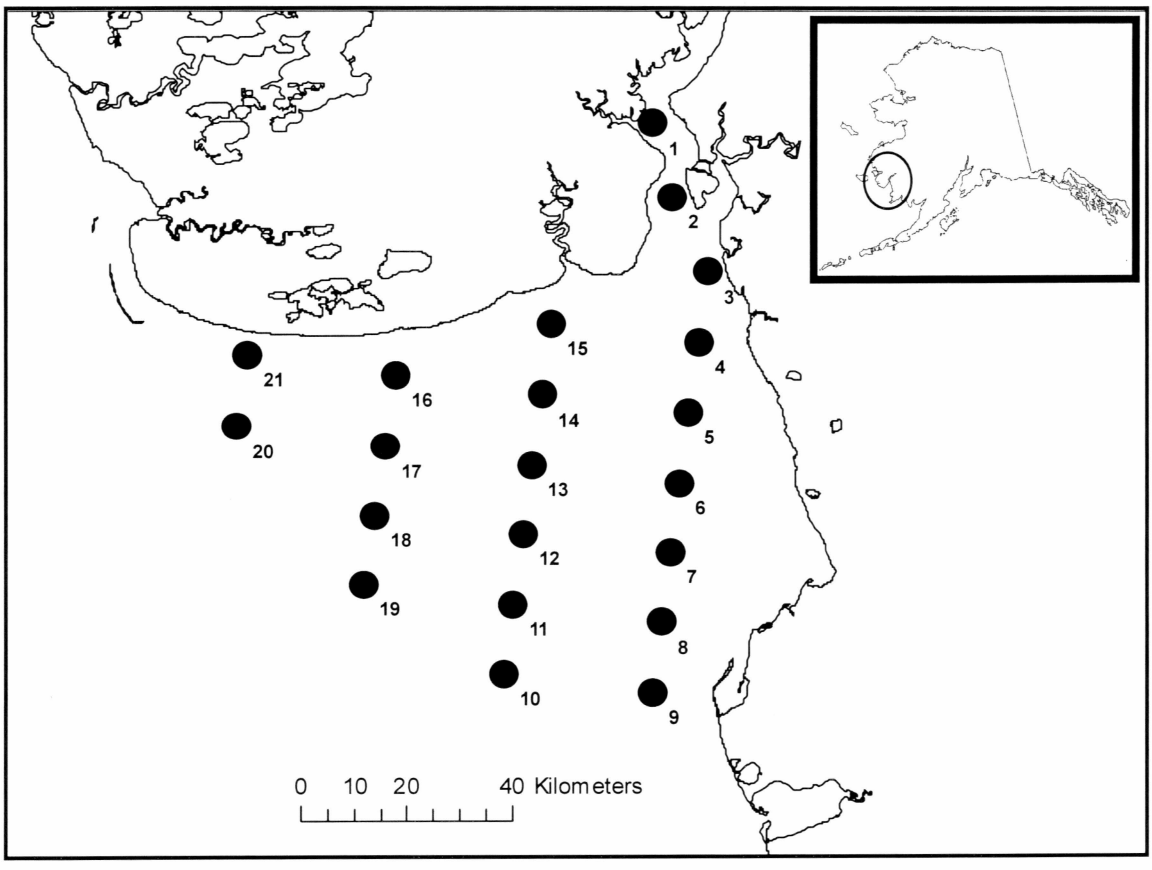

Figure 2.10. Kuskokwim Bay, Western Alaska. Sample area and stations locations for the 2003 and 2004 research cruises.

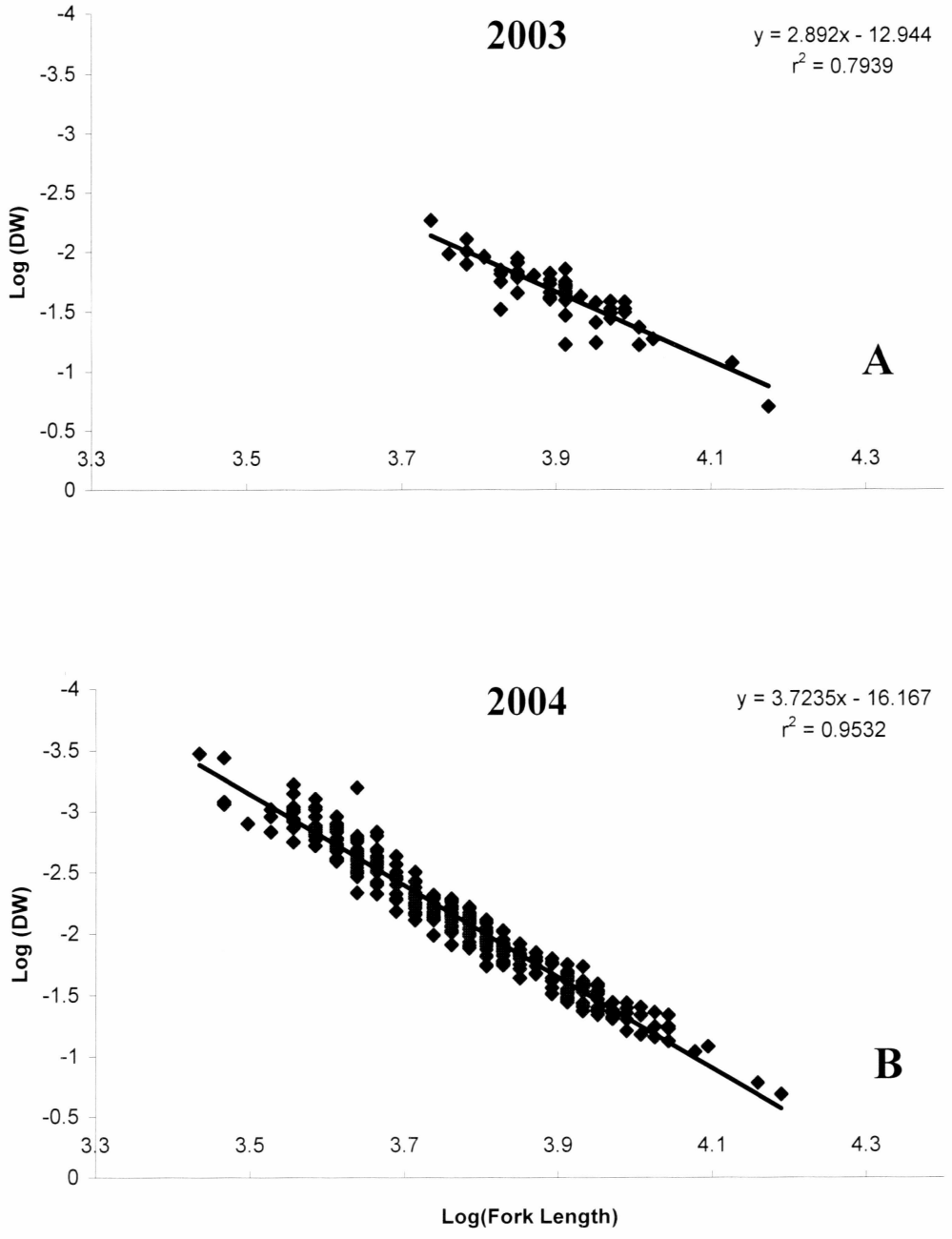

Figure 2.11. Linear regression of natural log of dry weight (DW) versus natural log of fork length for juvenile chum salmon from Kuskokwim Bay, in 2003 (A) and 2004 (B). n = 59 (A) and n = 291(B).

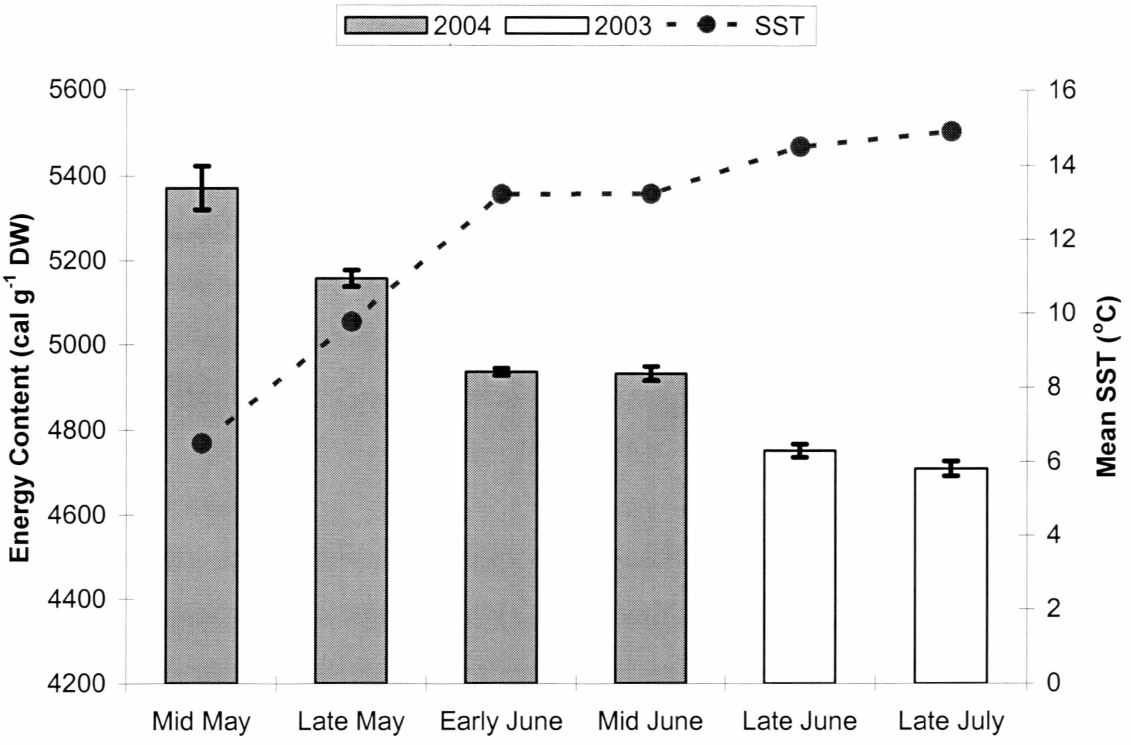

Figure 2.12. Comparison of juvenile chum salmon energy density by sampling period and sea surface temperature (SST) in Kuskokwim Bay for 2003 and 2004. Error bars represent ± 1 S.E. about the mean. Sample size is 11, 71, 182, 27, 56, and 3 for mid May until late July respectively.

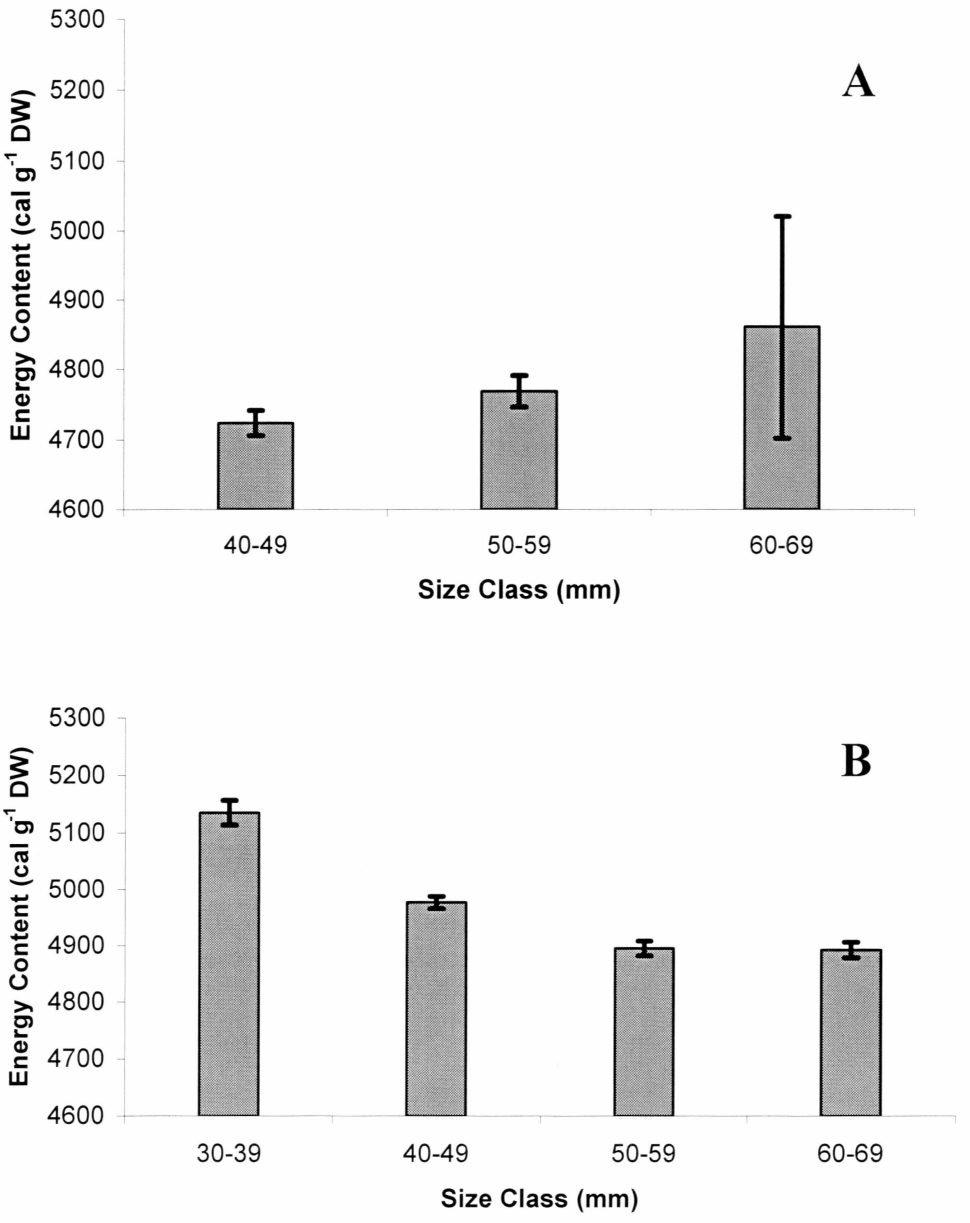

Figure 2.13. Interannual comparison of energy content between juvenile chum salmon of different size classes from Kuskokwim Bay, for 2003 (A) and 2004 (B). Error bars represent ± 1 S.E. about the mean. Sample sizes are 30, 27, and 2 (A) and 90, 132, 66, and 3 (B) for the 30-39, 40-49, 50-59, and 60-69 mm size classes.

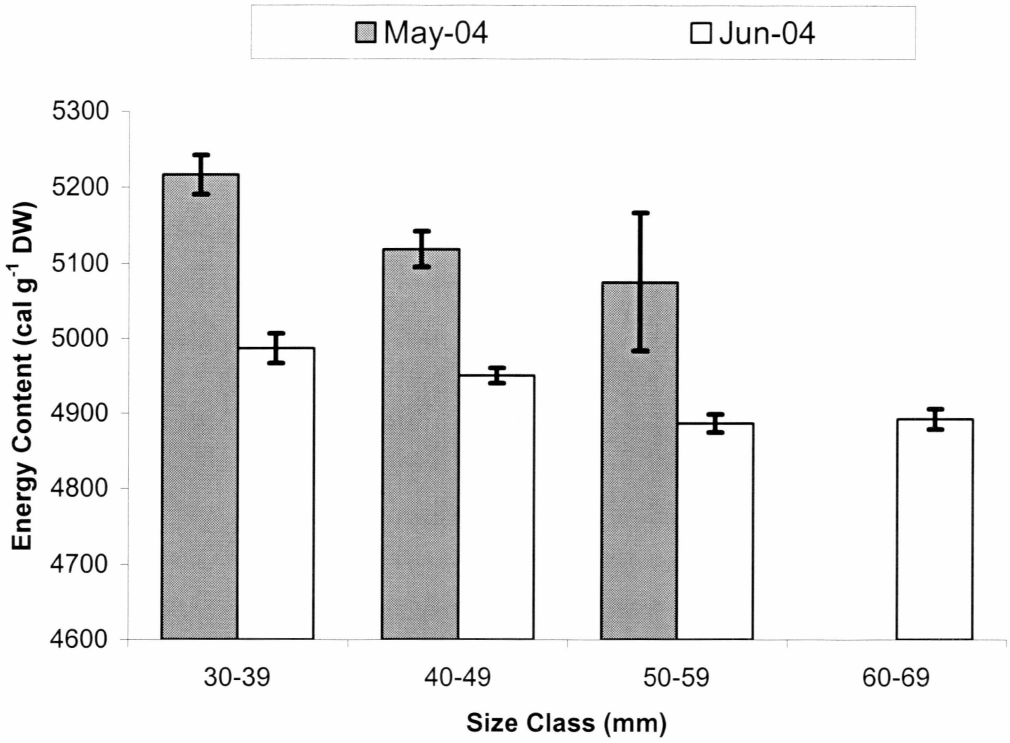

Figure 2.14. Seasonal energy content of juvenile chum salmon by size classes in Kuskokwim Bay. Error bars represent ± 1 S.E. about the mean. Sample sizes are 58, 21, and 3 in May, and 32, 11, 63, 3 in June for the 30-39, 40-49, 50-59, and 60-69 mm size classes.

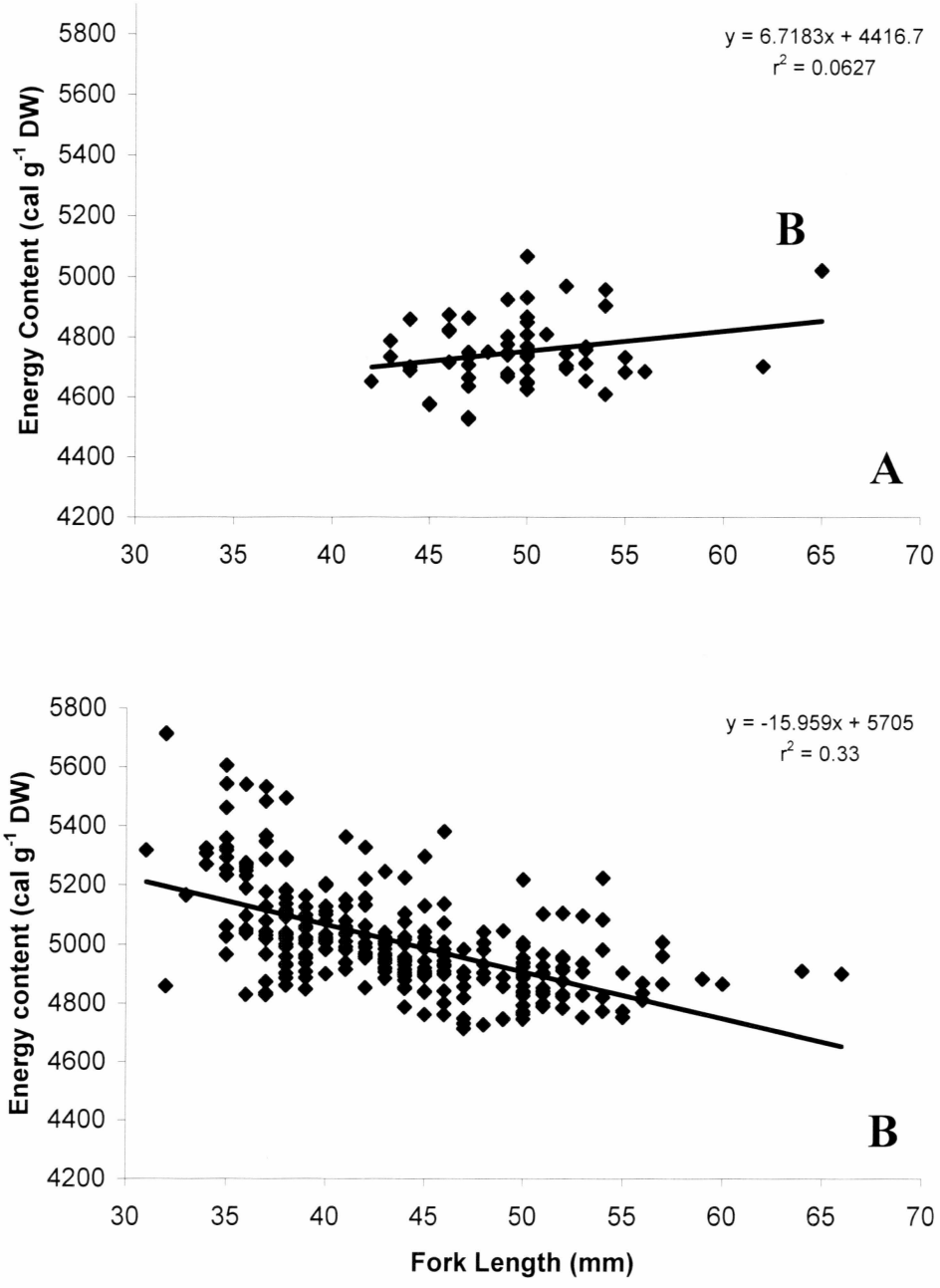

Figure 2.15. Linear regression of energy content versus fork length of juvenile chum salmon from Kuskokwim bay, in 2003 (A) and 2004 (B). n = 59 (A) and n = 291(B).

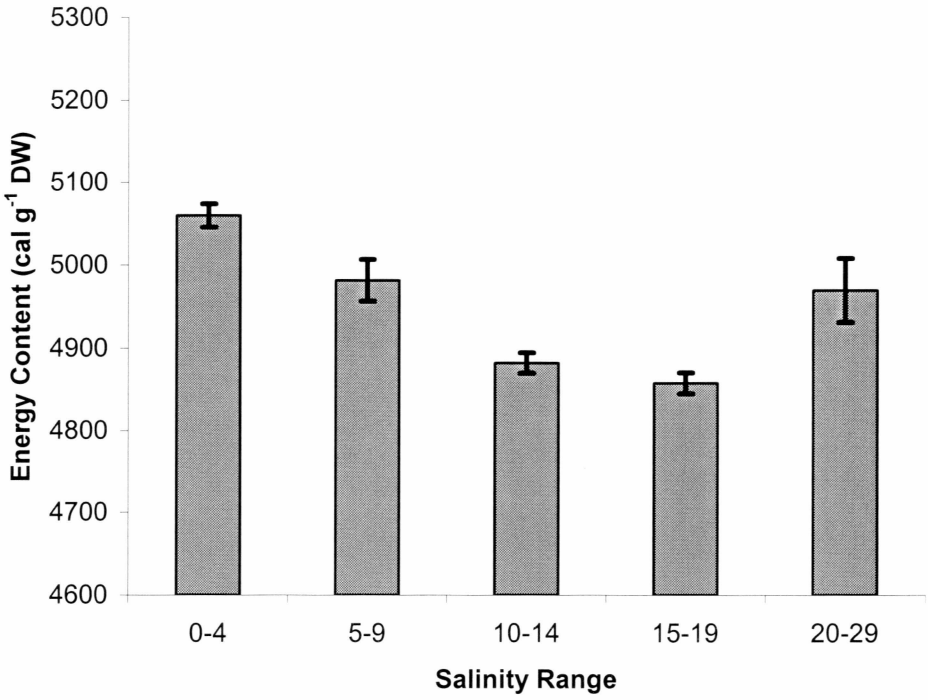

Figure 2.16. Comparison of energy content of juvenile chum salmon at different salinity ranges from Kuskokwim bay, 2004. Error bars represent ± 1 S.E. about the mean. Sample sizes are 164, 41, 28, 35, 4 for the salinity ranges from 0-4 until 20-29.

GENERAL CONCLUSION

The overall goal of this study was to assess the quality of Kuskokwim Bay as a nursery habitat for juvenile chum salmon. This was done by describing feeding success, diet composition, and patterns in energy density of juvenile chum salmon: 1) seasonally, by 2) fish size, and with changes in 3) salinity.

Smallest size classes of juvenile chum salmon were entering Kuskokwim Bay from the middle of May until the end of July. During this period, environmental conditions changed dramatically in the bay, impacting juvenile feeding patterns and energy density, and possibly leading to differential survival probabilities for juvenile chum salmon in Kuskokwim Bay.

Feeding success and dietary patterns of chum salmon juveniles were variable and differed with size, season, salinity, and year. Feeding incidence, i.e., the proportion of feeding juvenile fish, increased significantly with size and season. Numerical and weight-based feeding intensity increased with size class and week, and was highest in waters with moderate surface salinity ranging from 5 to 19. Feeding incidence and intensity were lowest for those juvenile chum salmon of the smallest size class that were collected early in the season and in water of 0-4 salinity.

Prey composition was similar between years; however, size classes, salinity ranges, and sampling weeks had an effect on the composition of gut contents. Small calanoid copepods (< 2.5 mm), harpacticoids, and drift insects were the primary prey items for juvenile chum salmon within the bay. Calanoids and insects combined made up > 50% of all prey consumed by chum salmon and > 80% of the overall prey biomass for all size classes, salinity ranges, and weeks. With the exception of a positive selection for small calanoid copepods, feeding by juvenile chum salmon in Kuskokwim Bay appeared to be mainly opportunistic. It should be noted, though, that our sampling design did not include a census of the benthic invertebrates or insects.

No significant diurnal feeding patterns were detected; however, mean weight of gut items was highest between 18:00 and 23:00 hours local time, and lowest at dawn (4:00 am). It is unlikely that sufficient time to detect a significant difference in diet

would occur at these high latitudes when there are only a few hours between sunset and sunrise in the summer months.

Mean energy content of chum salmon was significantly higher in 2004 than in 2003; however, since sampling in 2003 was conducted later in the season, the apparent interannual pattern in energy density might have been confounded by seasonal differences in energy density. Seasonal differences in energy density were apparent in 2004, when chum salmon energy density decreased from May to June. This decrease in energy densities from May to June in 2004 was observed for all size classes, except for fish $\geq$ 60 mm FL. In 2003, no significant differences in energy density were found with season, possibly due to low catches of juvenile chum salmon.

As juvenile chum salmon increased in size, their energy density significantly decreased. This pattern was detectable in both years of our study, but only statistically significant in 2004. The observed decrease in energy content with fish size might suggest that juvenile chum salmon were allocating the majority of their energy into somatic growth, rather than the storage of lipids. The significantly lower energy content of chum salmon of similar sizes outmigrating into the bay in June in comparison to May might be the result of higher metabolic costs, possibly due to higher sea surface temperatures. Seasonally increasing energy demands, particularly if not balanced by increasing food supply, could have severe implications for young fish, leading to declines in growth rates of chum salmon juveniles in Kuskokwim Bay.

No information exists about the possible population structure outmigrating cohorts of chum salmon juveniles in Kuskokwim Bay. If the sequence/pattern of outmigration timing is a function of chum salmon population structure, then it is likely that different smolt cohorts will experience differences in condition, growth, and likely survival probability. Future research in Kuskokwim Bay should further examine seasonal patterns in condition, growth, and mortality rates of different chum salmon cohorts. In addition, a better understanding of Kuskokwim River chum salmon populations is necessary to elucidate the effects of changing environmental conditions on differential

survival probabilities of chum salmon smolts during their estuarine residence in Kuskokwim Bay, Alaska.